

ECOLOGY

VOL. 32

JULY, 1951

No. 3

FORREST SHREVE

1878-1950

Forrest Shreve gave most of his productive life to the study of the deserts of North America and the relation of this desert vegetation to the factors of the environment. During the first half of this century he has occupied a position of prime importance in this field. He held faithfully to the objectives set up by the founders of the Desert Laboratory and his work was such as could be done only on plants growing under natural conditions. He held to the regional approach, a study of the structure, physiology and the natural history of the plant under natural conditions, all directed to the ultimate solution of the problems of the relation of the organism to its environment. It was the individual plant species rather than the complex plant community that appealed to Dr. Shreve for he found the relation of the plant to the environment much more important in the deserts than the relation of plant to plant. He was a field man, one who loved nature as he found it and strove to understand it and to interpret it to others. This interest and understanding he was able to instil into the minds of many of the younger men who worked with him when he was in charge of desert investigations.

Forrest Shreve began his botanical work at The Johns Hopkins University. Very soon his studies turned to the Montane Rain Forest in Jamaica in which he advanced our knowledge of transpiration and the means by which the vegetation of these tropical forests utilize the conditions of the environment. Soon he turned to the vegetation of Maryland, his native state, and later to the vegetation of the

United States. With this broad background he went, in 1908, to the Desert Laboratory at Tucson, Arizona established by the Carnegie Institution of Washington. Here he remained and worked until the time of his death.

His studies centered mostly on the Sonoran Desert and on the Chihuahuan Desert but extended to a Desert Mountain Range, a Coastal Mountain Range, and with Burton E. Livingston to the Distribution of Vegetation in the United States. About seventy titles of his papers are available to this author, mainly from the card catalog of the U. S. Department of Agriculture Library, and these are presented here as a bibliography to illustrate the scope of his interests, and his remarkable productivity as a scientist.

Dr. Shreve married Edith Coffin Belamy in 1909 well known and highly regarded for her work in plant physiology and whose counsel was exceptionally sound in this important field.

Born in Easton, Maryland July 8, 1878, Dr. Shreve died in Tucson, Arizona July 19, 1950 at the age of 72 years. He received the A. B. degree in 1901 and the Ph. D. degree in 1905 at The Johns Hopkins University. He was Associate Professor of Botany at Goucher College, 1906-1908, Staff Member, Department of Botanical Research Carnegie Institution, 1908-1927, and in charge of Desert Investigations since 1928. In 1911 he became Managing Editor of *THE PLANT WORLD*, and continued the work through 1919, until that journal was taken over as the official organ of The Ecological Society of America. To this day, the front

cover of *ECOLOGY* carries the line "Continuing The Plant World." THE PLANT WORLD played an important part in the field of plant ecology during these years. Shreve was one of the founders of the Ecological Society of America, was secretary-treasurer 1915-1919 and president in 1921. In 1926 he was editor of the *Naturalists Guide to the Americas*.

He was an active member of many scientific societies including the following: fellow in the American Association for the Advancement of Science; member of the Botanical Society of America; the Ecological Society of America; the American Society of Naturalists; the Association of American Geographers; the Society of American Foresters; and the California Botanical Society. The VII International Botanical Congress in Stockholm in 1950 selected him as one of the Honorary Presidents of the Congress, and he was a member of Phi Beta Kappa and Sigma Xi.

The following bibliography is thought to be very nearly complete.

H. L. SHANTZ
454 PASEO DEL DESCANSO
SANTA BARBARA, CALIFORNIA

BIBLIOGRAPHY OF ARTICLES
BY FORREST SHREVE

1904. Some plants which entrap insects. *Pop. Sci. Month.* 65: 417-431.
1905. The development of *Sarracenia purpurea* L. *Johns Hopkins Univ. Circ.* 1905 (5): 31-34.
1906. A collecting trip at Cinchona (Jamaica). *Torrey* 6: 81-84.
The development and anatomy of *Sarracenia purpurea*. *Bot. Gaz.* 42: 107-126.
The Hope Botanical Gardens (Kingston, Jamaica). *Plant World* 9: 201-207.
A winter at the tropical station of the Garden (Cinchona, Jamaica). *Jour. New York Bot. Gard.* 7: 193-196.
1907. Studies on rate of growth in the mountain forests of Jamaica. *Johns Hopkins Univ. Circ.* 1907 (3): 31-37.
1908. Transpiration and water storage in *Stelis ophioglossoides* Sw. *Plant World* 11: 165-172.
1910. The ecological plant geography of Maryland. *Maryland Weather Service* 3: 101-148, 199-219, 275-292.
- The floristic plant geography of Maryland. *Maryland Weather Service* 3: 65-97.
- (—, M. A. Chrysler, F. H. Blodgett, and F. W. Besley.) The plant life of Maryland. *Johns Hopkins Univ. Press.*
The rate of establishment of the giant cactus. *Plant World* 13: 235-240.
- The relation of natural vegetation to crop possibilities. *Maryland Weather Service* 3: 295-303.
- The coastal deserts of Jamaica. *Plant World* 13: 129-134.
1911. Establishment behavior of the palo verde. *Plant World* 14: 289-296.
The influence of low temperature on the distribution of the giant cactus. *Plant World* 14: 136-146.
Studies on Jamaican Hymenophyllaceae. *Bot. Gaz.* 51: 184-209.
1912. The investigation of a climatic gradient (abstract). *Sci.* 35: 157-158.
Cold air drainage. *Plant World* 15: 110-115.
(Livingston, Burton E., and —.) The relation between climatic conditions and plant distributions in the United States. *Johns Hopkins Univ. Circ.* 1912: 129-130.
1913. A guide to the salient physical and vegetational features of the vicinity of Tucson, Arizona. No publisher; 11 pp.
1914. The role of winter temperatures in determining the distribution of plants. *Amer. Jour. Bot.* 1: 194-202.
The direct effects of rainfall on hygrophilous vegetation. *Jour. Ecology* 2: 82-98.
A montane rain-forest; a contribution to the physiological plant geography of Jamaica. *Carnegie Inst. Washington Pub.* 199.
Rainfall as a determinant of soil moisture. *Plant World* 17: 9-26.
1915. The vegetation of a desert mountain range as conditioned by climatic factors (Santa Catalina Mts., Arizona). *Carnegie Inst. Washington Pub.* 217.
1916. The weight of physical factors in the study of plant distribution. *Plant World* 19: 53-67.
Experimental work at Cinchona (Jamaica). Page 919 in *Cinchona as a tropical station for American botanists. Sci.* 43: 917-919, by Duncan S. Johnson.
1917. The establishment of desert perennials. *Jour. Ecology* 5: 210-216.
A map of the vegetation of the United States. *Geog. Rev.* 3: 119-125.
The physical control of vegetation in rainforest (Jamaica) and desert moun-

- tains (Santa Catalina Mts., Arizona). *Plant World* 20: 135-141.
1918. The Jamaican filmy ferns. *Amer. Fern Jour.* 8: 65-71.
1919. A comparison of the vegetational features of two desert mountain ranges (Pinaleno Mts. and Santa Catalina Mts. of southern Arizona). *Plant World* 22: 291-307.
1921. (Livingston, Burton E., and —.) The distribution of vegetation in the United States, as related to climatic conditions. *Carnegie Inst. Washington Pub.* 284.
1922. Conditions indirectly affecting vertical distribution on desert mountains (mountains of southwest U. S.). *Ecology* 3: 269-274.
1924. The growth record in trees. Pages 89-116 in *Growth in trees and massive organs of plants* (by MacDougal, D. T., and —.). *Carnegie Inst. Washington Pub.* 350.
- Across the Sonoran Desert. *Bull. Torrey Bot. Club* 51: 283-293.
- Soil temperature as influenced by altitude and slope exposure. *Ecology* 5: 128-136.
1925. Ecological aspects of the deserts of California. *Ecology* 6: 93-103.
1926. The desert of northern Baja California. *Bull. Torrey Bot. Club* 53: 129-136.
1927. The vegetation of a coastal mountain range (Santa Lucia Mts., California). *Ecology* 8: 27-44.
- The physical conditions of a coastal mountain range (Santa Lucia Mts., California). *Ecology* 8: 398-414.
- Soil temperatures in redwood and hemlock forests. *Bull. Torrey Bot. Club* 54: 649-656.
1929. Changes in desert vegetation (near Tucson, Arizona). *Ecology* 10: 364-373.
1931. The cactus and its home. *Williams & Wilkins Co.* Baltimore.
- Physical conditions in sun and shade (near Tucson, Arizona). *Ecology* 12: 96-104.
1933. (—, and T. D. Mallery.) The relation of caliche to desert plants. *Soil Sci.* 35: 99-113.
1934. The desert and its life. *News Service Bull. Carnegie Inst. Washington* 3: 115-119.
- The problems of the desert. *Sci. Monthly* 38: 199-209.
- Vegetation of the northwestern coast of Mexico. *Bull. Torrey Bot. Club* 61: 373-380.
1935. A desert by the sea (Lower California). *Desert* (Pasadena, California) 7: 127-128.
- The longevity of cacti. *Cactus & Succulent Journal* 7: 66-68.
- Nordamerikanische Wüstenpflanzen II, Die Pflanzenareale. Vierte Reihe, Heft* 3: 17-24.
1936. The plant life of the Sonoran Desert. *Sci. Monthly* 42: 195-213.
- (—, and W. V. Turnage.) The establishment of moisture equilibrium in soil. *Soil Sci.* 41: 351-355.
- The transition from desert to chaparral in Baja California. *Madroño* 3: 257-264.
1937. Plants of the sand. *News Service Bull. Carnegie Inst. Washington* 4: 91-96.
- (—, and A. L. Hinckley.) Thirty years of change in desert vegetation (near Tucson, Arizona). *Ecology* 18: 463-478.
- The vegetation of the cape region of Baja California. *Madroño* 4: 105-113.
- Lowland vegetation of Sinaloa. *Bull. Torrey Bot. Club* 64: 605-613.
1939. Observations on the vegetation of Chihuahua. *Madroño* 5: 1-13.
- (Moore, George T., C. S. Gager, and —.) Daniel Trembly MacDougal, pioneer plant physiologist. *Plant Phys.* 14: 191-202.
1940. The edge of the desert (N. Amer. desert, distrib. of *Larrea divaricata*). *Yearbk. Assoc. Pacific Coast Geog.* 6: 6-11.
1942. The desert vegetation of North America. *Bot. Rev.* 8: 195-246.
- Grassland and related vegetation in northern Mexico. *Madroño* 6: 190-198.
- Vegetation of northern Mexico (abstract). *Yearbk. Assoc. Pacific Coast Geog.* 8: 3-5.
- The vegetation of Jamaica. *Chron. Botanica* 7: 164-166.
- The life forms and flora of the North American desert. *Proc. Amer. Sci. Congr.* 8th, Washington, 1940, 3: 125-132.
1944. Rainfall of northern Mexico. *Ecology* 25: 105-111.
1945. The saguaro (*Cereus giganteus*) cactus camel of Arizona. *Nat. Geog. Mag.* 88: 695-704.
1951. Vegetation of the Sonoran Desert. Vol. I. Vegetation. *Carnegie Inst. Washington Pub.* 591 (in press).

INTERRELATIONS OF CERTAIN PHYSICAL AND CHEMICAL FEATURES IN A HEADWATER LIMESTONE STREAM¹

JOE KENDALL NEEL

U. S. Public Health Service, Kansas City, Missouri

The three forks (North, Middle, and South Fork) of the Kentucky River drain the south central section of the eastern Kentucky coal fields and unite to form the main river in the vicinity of Beattyville. From the junction of its forks, the river flows northwest into the central bluegrass region, bends rather sharply southwest a short distance downstream from Boonesboro, and turns northwest again in the vicinity of Camp Nelson, in Jessamine County. For a considerable distance above and below Frankfort, the Kentucky flows almost directly north, but finally bends to the west to join the Ohio at Carrollton. In their journey from the northwestern slopes of the Cumberland Mountains through the bluegrass to the Ohio, the waters of the Kentucky River pass over a considerable variety of rocks and other minerals. In the bluegrass region the river flows over, by, and even under various strata of limestone. Several smaller streams that enter the Kentucky in this area have limestone beds their entire lengths, except possibly for short distances along upland pasture brooks, but these brooks owe their origin to springs that emerge from limestone strata in the majority of instances. These creeks are known locally as limestone streams, and, although they flow into the Kentucky near its middle, their size marks them as headwater streams.

The University of Kentucky, at Lexington, is located near several limestone streams of varying sizes. The stream research program that has been established by the Department of Zoology has studies of these streams as its first objectives, with later ramifications to include various

types of streams in sundry localities, the ultimate objective being knowledge of factors that control biological productivity of streams in general.

Studies of streams in Kentucky have not been common. Allen (1945) discusses the economic, cultural, and recreational aspects of streams in the state, pointing out conflicts among various uses of streams, and urging some system of unified management based upon scientific knowledge. Mussels in Kentucky streams have been dealt with by Wilson and Clark (1912, 1914), Danglade (1922), Ortmann (1926), Clench and van der Schalie (1944), and Call (1896). Kentucky stream fishes have been studied by Rafinesque (1820), Kirtland (1841, 1845), Putnam (1872), Jordan and Brayton (1877), Jordan and Swain (1883), Kirsch (1892, 1893), Woolman (1892), Garman (1894), Call (1896), Evermann (1902, 1918), Hubbs (1927), Howland (1931), Welter (1938), Neel (1938), Smith (1942), and Allen and Clark (1943). Clarke (1924) furnishes chemical analyses of waters from Elkhorn Creek, Green River, Kentucky River, and Cumberland River. Kofoid (1900) was concerned with plankton of the Echo River, Mammoth Cave.

Limnological studies of streams have been far less numerous than those dealing with the standing water series, and understanding of various factors operative in streams is much less detailed than that dealing with various phases of lentic biology and dynamics. The publications of Kofoid (1903, 1908), Steinmann (1907), Thienemann (1912), Galtsoff (1924), Behning (1927), Muttkowski (1929), Richardson (1921), and a few others resulted from studies of rather generalized

¹Contribution from the Department of Zoology, University of Kentucky.

features of the lotic environment. Recently, Berg (1943, 1948) has gone into greater detail on physiographical, physical, chemical, and biological features of the

River Susaa in Denmark. Less lengthy papers on streams are more numerous, and those known to have bearing on this investigation will be mentioned later.



FIG. 1. Outline map of Boone Creek basin, showing locations of stations, roads, and habitations.

The present report is based upon physical and chemical data obtained in conjunction with studies on plankton, periphyton, and certain fishes in the middle-sized limestone stream described below. Analyses made upon this stream, due to their frequency and concentration, have furnished a more detailed and basic picture of certain physical and chemical stream dynamics than is described in any paper known to the author.

Expenses for field work and equipment needed in this problem were provided by a grant-in-aid from the University of Kentucky Research Fund, and by the Department of Zoology. A few items of equipment were made available through war surplus. The author is indebted to W. R. Allen, Professor of Zoology, for valuable assistance in establishing the early phases of the stream program, for certain bibliographical help, and for photographs appearing herein. Thanks are also due Bromfield L. Ridley and Keith V. Slack for bringing samples from the stream upon three occasions when circumstances prevented their collection by the author.

STREAM AND REGIONS STUDIED

Boone Creek, our "type" stream, situated 12 miles east of Lexington, Kentucky, forms part of the boundary between Fayette and Clark Counties (Fig. 1). Beginning as small spring-fed brooks in bluegrass pastures this stream cuts approximately 400 feet through Ordovician limestone in its 15 mile passage to the Kentucky River. Though no industrial wastes empty into its drainage it cannot technically be considered unpolluted, as it receives domestic sewage and farm wastes from the villages and farms shown in Figure 1. The greater portion of land in this basin is in pasture and the banks are appreciably wooded only in middle and lower regions where precipitous cliffs and bluffs occur. Practically no forest drainage enters the stream. Areas in cultivation are usually situated among pastures and there is relatively little direct runoff across plowed fields. Quantities of silt present

in the water are therefore never very great. In upper regions calcium diphosphate rock and chert occur superficially.

The region of the stream first selected for intensive study is situated near Grimes Mill, which is below the entrances of all but one major tributary. In this section the creek is made up of alternating riffles and pools, with bottoms composed mainly of limestone bedrock and rubble. The banks are largely tree-covered and much of the water is well shaded during the verdant months. Considerable seepage water from the surrounding bluffs enters the stream here during winter, spring, and early summer, and some springs with considerable flow (up to 7200 cu. ft. per hour in spring) normally persist the entire year. Some flow through the bluffs and cliffs enters below the surface of the stream, as will be mentioned later, but in many cases the springs and seepage areas break through the surface of the earth some distance above the stream. Four stations were established for routine sampling in this area.

Station 1 includes the normally shallow stretch of water immediately below the

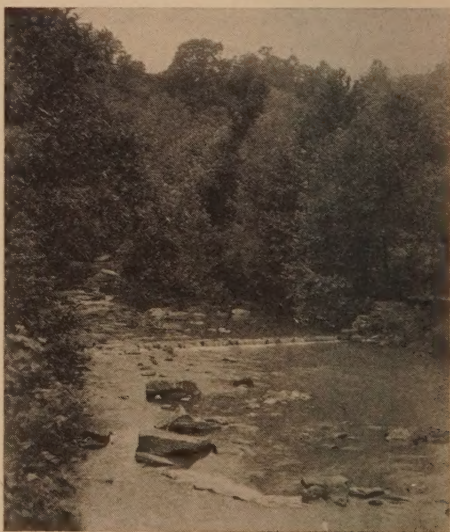


FIG. 2. Looking upstream at Station 1 during early summer, 1949.

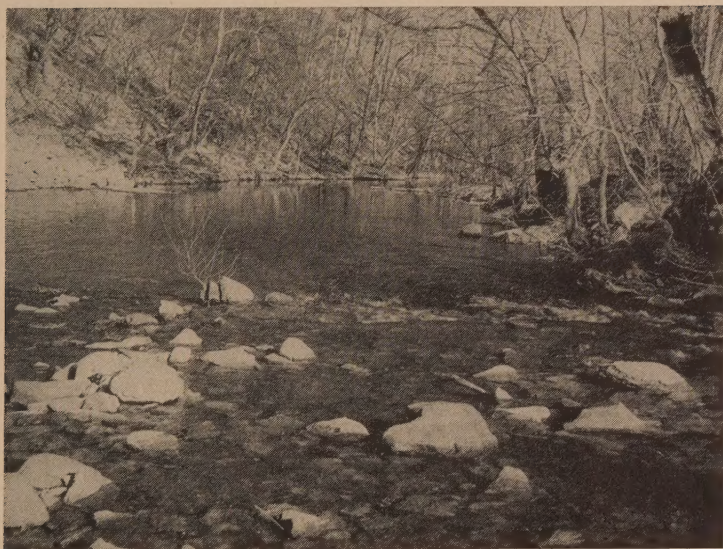


FIG. 3. Station 2, the riffle in foreground, and Station 3, the pool beyond.

ruins of the Grimes Mill dam (Fig. 2), which consists of a pool to the left and a riffle to the right when water is flowing over only part of the dam, and becomes a rapids for its entire width when flow is over all the dam. Above the dam the creek forms a long, narrow, well shaded stretch of water that is mainly riffle. The stream widens abruptly to 68 feet at the dam and averages almost 50 feet in width for almost a hundred yards below. Water here is well shaded near the right bank but exposed on the left. The bedrock of the bottom is barren from left bank to mid-stream, but from that point to the right bank is overlaid with large rocks and other rubble. About 50 feet below the dam, bare bedrock forms the entire bottom. During low stages of the stream, flow is across the right side of the dam and down over the rubble. During the fall of 1949 the dam remnants from left bank to center were removed. Just what effects this action will have upon certain physical features at Station 1 remain to be seen. However, it has resulted in altered current patterns with formation of an eddy up the left bank that has deposited sand and

other materials that were not there before. Depth at Station 1 has varied from extremes of no water to four and one half feet.

Station 2, a riffle 340 feet downstream from Station 1, has a maximum width and length of 50 and 72 feet, respectively, with bottom formed of a considerable deposit of large and medium sized stones in which is mixed sand- and gravel-sized rubble of chert and limestone (Fig. 3). Deepest water and greatest flow are along the right bank, and water here is well shaded except on the extreme left. Depth at this station has varied from 0 to slightly less than 5 feet. The section of stream between the first two stations consists of riffle with the exception of a small pool just above the second station. Bare bedrock forms the bottom over the entire 340 feet.

Water flows from Station 2 directly into Station 3, a pool 280 by 40 feet (Fig. 3). The entire bottom is barren bedrock except for some rubble at the tail and some spots of eddy-deposited sand and gravel at the head. Flow through the pool is mainly to left of center, veering toward the right bank with falling water level.

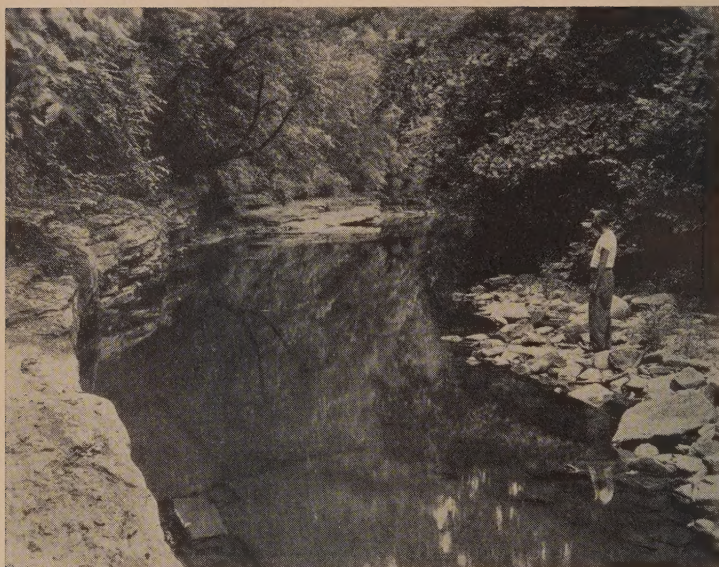


FIG. 4. Station 4 in late summer, 1949.

About 75 feet above the tail, a sudden narrowing of the stream bed forms a strong eddy back up the right side during periods of high water. Weaker eddies are often evident near the head of the pool at the left. Quantities of sand and gravel are dropped near the head of the pool by the strong eddy up the right, but this material is later eroded when the downstream current moves right. Fine rubble and organic debris deposited on the left by the weaker eddies is frequently removed by higher stream stages. Although surrounded by trees, about one-half the area of Station 3 is exposed to the sun most of the day. Depth varied from 0-6 feet, the latter figure representing a very high water level. Usual depth was about two feet.

Station 4, another pool, is situated 675 feet below Station 3 (Fig. 4). The intervening stretch is well shaded and consists of two pools with bare bedrock bottoms and three riffles, two with rubble bottoms and the third with bedrock. Long and curved (750 $\times$ 50 feet), Station 4 is considerably greater in area than Station 3, and the usual depth is about three feet.

The entire left bank is formed by a low undercut cliff with successive ledges dropping off into deeper water near the center. The right bank is low and tree covered, and the upper part of the pool is well shaded during verdant months. The lower third of the pool is exposed to sunlight over the greater part of the day, even when vegetation is most luxuriant. The main flow is along the left bank, and a very strong eddy courses up along the right bank during higher water levels. This eddy owes its origin to a sudden narrowing of the pool near the center, and along its course of some 300 feet upstream deposits considerable quantities of sand, gravel, silt, and organic detritus near the right bank. Silting is noticeable near the middle and toward the lower end of the pool. Several large fissures occur in bedrock near the stream center. Near the tail of the pool rubble has been built up in ridges running parallel to the length of the stream.

After sampling at these four locations from July, 1948 to September, 1949, a necessity for studies further upstream be-

came evident and six more stations were established at the sites shown in Figure 1. Station 5 includes the pool and riffle, shown in Figure 5, located just east of the Cleveland Road. The pool bottom is bedrock overlaid with mud except near the head, where it is barren. The riffle bottom consists of small rocks and gravel for the most part, although large pieces of limestone are scattered about in both riffle and pool. Further details may be gained from study of the photograph (Fig. 5) made during late winter.

Stations 6, 7, and 8 are typical upland pasture brooks. Station 6 is shown in Figure 6, and many of its features are evident in the photograph. These brooks all have earthen banks and bottoms of chert and limestone rubble or limestone ledges. Phosphate rock seldom occurs in the streams or in their banks. Station 9 is the smallest stream that has been visited routinely. Here the banks are of earth and the bottoms of clay and silt, while the stream varies from 3-6 feet in width. Flow from two springs forms the brook at the sampling station, and the lower of the two is shown in Figure 7. The rill be-

low the spring has been enlarged to form the small stock pond shown in the foreground. Station 10 (Fig. 8) was established on what appears to be a typical mid-stream section of Boone Creek. The creek is wide and shallow in this region, with earthen banks and gravel and limestone bottom. Many small springs enter the stream just above the water level, two just below the sampling kits shown in the photograph. Other details are evident in the figure.

Other small brooks of the upper region have been sampled, particularly those that begin as springs, and waters from the springs have been analyzed. These additional samples have included little routine collection at any one site. The largest spring in the Boone Creek system is historic Basin Springs, which has formed a pool almost 400 square feet in area and 4 feet deep where it flows out and up from a limestone cavern. During the spring-time the pool discharges approximately 7200 cubic feet per hour by a rill which joins another tributary 500 feet below. Eight springs in all have been visited, but only three routinely.



FIG. 5. Station 5 in late winter.



FIG. 6. Station 6 in early spring.

From early spring until high water in late fall most riffles in the Grimes Mill section have their bottoms covered with benthic algae, the constitution and quantity of which vary from time to time.

This growth is designated as periphyton following the usage of Young (1945), and will be the subject of a later paper, though certain of its influences upon the chemistry of the water will be dealt with here.



FIG. 7. Lower spring and pool at Station 9.

Periphyton has been less developed on the rapids above Station 1 than at Station 1 or on the riffle below, where benthic algae are frequently very dense. Algal growth has been less luxuriant at Station 2, and in Station 3 is usually represented by very few forms. Between the third and fourth stations periphyton becomes well developed on the riffle with bedrock bottom and in the lower of the two pools, shortly above Station 4. Small areas in the other two riffles sometimes exhibited dense growths. In the upper branches (Stations 5-10 and

and in them measurements were from surface to bottom, with allowance for surface disturbance. Temperature was at first measured with a maximum-minimum thermometer and later with a Foxborough resistance thermometer. When the bulb of the latter was lowered in a horizontal position it was possible to detect temperature differences in thin layers of water. A turbidimeter was not available until near the end of the period covered in this report and measurements of turbidity are not given herein. Chemical analyses



FIG. 8. Station 10 in early spring.

other small streams) periphyton is very successful. The majority of algae found in the stream (*Lemanea*, *Cladophora*, *Oscillatoria*, *Phormidium*, diatoms, etc.) belong in the periphyton, but in some of the smaller streams dense, floating, blanketing growths of *Spirogyra* occur.

METHODS OF STUDY

Height of water was at first determined by measuring down to the surface of one of the pools from a bench mark established on the ledge above. It was later found desirable to ascertain depths in rapids,

were according to the usual methods (American Public Health Association 1936). The azide modification of the Winkler method was used for oxygen determinations.

Methyl orange alkalinity as used here is based upon the amount of standard acid ($N/50 \text{ H}_2\text{SO}_4$) required to reduce pH from the endpoint of phenolphthalein (8.0) to that of methyl orange (4.0) when pH exceeded 8.0. When pH was below 8.0 methyl orange alkalinity was, of course, total alkalinity. Customary usage of methyl orange alkalinity makes it synony-

mous with total alkalinity, no matter what the beginning pH value; but, since it appeared desirable to preserve original titration values in this paper and still show differences in monocarbonate and bicarbonate content, this liberty was taken in delimiting the range of methyl orange alkalinity. Total alkalinity, i e., customary methyl orange alkalinity, may be arrived at by adding phenolphthalein and methyl orange alkalinity values in tables.

Phosphate was measured in an electrophotometer, using ammonium molybdate and stannous chloride for development of color. Sampling was at weekly intervals with few exceptions. Records for the Grimes Mill region cover a period of 21 months (July, 1948, through March, 1950), while those for the upper portion represent only a 7-month period (September, 1949, through March, 1950). Their inclusion in this paper brings additional evidence to bear upon certain relationships brought out in downstream studies. To date, studies of the upper creek are adjudged incomplete for purposes other than supplementing data obtained in the Grimes Mill section.

PHYSICAL FEATURES

Water level variation

Early in the course of this study it was found impracticable to measure water level at one position and assume that any rise or fall shown there would be indicative of water level change throughout the stream. Seldom did different regions show comparable rise or fall, and pools and rapids usually differed markedly in height of water level for any given rate of flow. Eddies in pools are chiefly responsible for this discrepancy, for, when these back currents are not present, water level changes in pools and rapids usually correspond. During a large part of the year eddies are present and so normally need to be considered. They are formed by any feature of the stream bed that tends to obstruct flow, such as a sudden narrowing near the middle or tail of a pool, a large

piece of limestone upthrust from the bottom, or bars or large rocks extending out into the stream. When rate of flow is low, there is little pile-up at obstructions and back-flow is very slight or nonexistent; and when the stream is very high, pools lose their character and eddies are very infrequent in the rushing layer of water that occupies the stream bed from bank to bank.

The general tendency of eddies in pools is to magnify the general rise or fall that may be measured on rapids. The fact that stream level may be either too high or too low for eddy production permits recognition of upper and lower stream level thresholds between which eddies will be formed. It is hardly necessary to add that these thresholds differ in various pools. When stream levels enter the range for eddy formation from either above or below, the magnifying effect is much more pronounced than when water level fluctuations occur between upper and lower limits. For instance, records show a rise of 4 inches in Station 2 to be accompanied by a rise of 10 inches in Station 3, and a subsequent drop of 6 inches at Station 2 to correspond to a fall of 12 inches in Station 3 when water level passed above and below the lower threshold for eddy occurrence. At corresponding times Station 4 attained an increase of only 7 inches and later fell but 8 inches.

Pools are unreliable sites for water level studies and changes noted on rapids represent more accurately variation in rate of flow. Some pools are very poor indicators of general conditions, even when eddies are not present. Such pools are located to one side of the main path of flow, seldom form eddies, and usually exhibit less water level variation than the neighboring rapid. When flow is greatly reduced, pools of this nature usually become completely isolated from the rest of the stream. During very low stages of Boone Creek the rapids served mainly to maintain pool levels, since, upon one occasion, these exhibited little drop for a few days after the rapids dried completely.

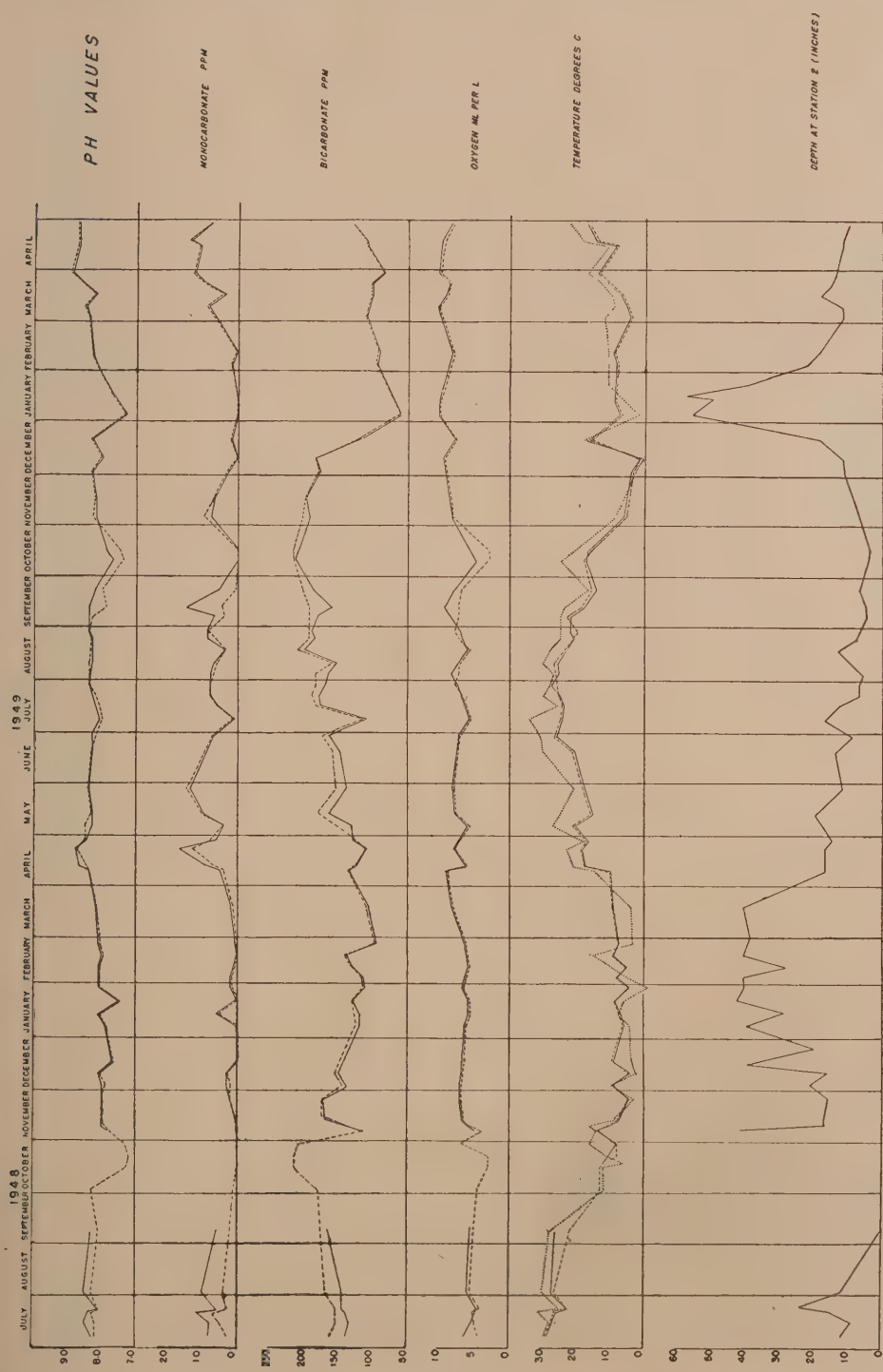


Fig. 9. Variation in stream level as associated with temperature and certain chemical features of surface water at the four Grimes Mill stations. Riffles are shown by solid lines, pools by broken lines, and air temperature by a dotted line.

Annual variation. Flow ceased in early September, 1948, and by late October of that year the stream had dried down to scattered pools. Heavy rains filled it overnight on November 5, and a period of heavy flow continued until the latter half of March, 1949. During the summer of 1949 flow was mainly in middle ranges for this creek. A period of low water stages began in late August and continued until early December, but, unlike 1948, the riffles did not become dry. The high-water period beginning in December, 1949, has continued to the present (April, 1950), although drops to middle stream levels have occurred. For the period covered by this report, times of low water are decidedly few, as shown in Figure 9. Station 2 was finally selected as the site of depth measurements and during the 21-month period water varied from 0 to 58 inches. Here depths of 36 inches or greater were sufficient to wipe out distinctions between riffles and pools, and give a rushing torrent of water over the entire width of the stream bed, and even beyond.

Temperature and thermal stratification

During 1948 and 1949, highest water temperatures occurred with highest air temperatures in July. Study of Figure 9

will show that water temperatures had the general decline and rise exhibited by air temperatures over the seasons, but that they frequently differed considerably over more limited periods of time. At the first four stations water never attained the temperature extremes exhibited by air and at times differed as much as 18° F. Upon many occasions stream temperatures did not very closely approach those of the air, and diurnal variation was always over a more limited range than that of the air. Air temperature differed from station to station, reflecting the variation in shade along this stretch of stream. In upland brooks water temperature frequently exceeded that of the air.

Surface water temperatures normally differed slightly in pools and rapids but varied considerably in different sections of the stream. Longitudinal non-uniformity of temperature may be due to variation in exposure to the sun or to increase and decrease in width of stream bed. A wide area of stream bed exposes more surface per volume than a narrow channel for any given rate of flow, with the result that water is more readily warmed or cooled when passing over wide shallow areas. The sudden widening of the stream from 25 to 68 feet at the dam above Station 1 greatly increased surface exposure,

TABLE I. *Temperature and dissolved oxygen at Stations 1-4 over summer, fall, and early winter, 1949*

Date	Station 1		Station 2		Station 3				Station 4			
					Surface		Bottom		Surface		Bottom	
	Temp. ° F.	O ₂ ml. per l.	Temp. ° F.	O ₂ ml. per l.	Temp. ° F.	O ₂ ml. per l.	Temp. ° F.	O ₂ ml. per l.	Temp. ° F.	O ₂ ml. per l.	Temp. ° F.	O ₂ ml. per l.
July 28	79	8.5	82	7.6	82	8.3	80	8.0	—	—	—	—
Aug. 4	74	7.7	78	8.5	79	7.7	74	6.2	77	7.4	73	6.1
Aug. 10	78	7.6	78	7.6	80	7.6	78	7.6	—	—	—	—
Aug. 18	74	6.2	74	7.4	78	7.3	74	6.6	—	—	—	—
Aug. 25	70	7.0	72	7.6	72	7.6	72	7.6	72	—	72	—
Aug. 29	72	7.3	72	7.8	73	7.8	72	7.6	—	—	—	—
Sept. 7	69	7.7	72	8.7	72	8.2	69	7.7	70	7.7	67	6.5
Sept. 12	64	9.0	66	9.7	64	8.4	60	7.5	64	7.1	60	6.6
Sept. 23	58	7.7	58	8.7	60	7.3	58	7.3	62	7.0	58	6.5
Oct. 8	63	4.8	64	5.4	65	3.1	63	3.1	—	—	—	—
Oct. 14	64	5.0	64	7.0	63	3.2	62	3.0	—	—	—	—
Nov. 5	44	8.5	44	8.6	47	8.6	44	8.6	48	8.6	44	8.6
Dec. 2	40	9.5	40	9.5	39	9.5	39	9.5	39	9.5	39	9.5
Dec. 21	62	8.0	62	8.0	62	8.0	62	8.0	62	8.0	62	8.0

TABLE II. *Selected vertical thermal patterns at Stations 3 and 4. Temperatures are in degrees Fahrenheit*

Depth	Station 3						Station 4					
	July 7, '48	July 15, '48	Aug. 2, '48	Aug. 5, '49	Aug. 18, '49 (5" Rise)	Sept. 7, '49	July 15, '48	Aug. 2, '48	Oct. 15, '48 No flow	Aug. 5, '49	Aug. 18, '49 (5" Rise)	Sept. 7, '49
Surface	84	81	78	80	74.5	72	80	76	54	77	74.5	70
4 inches	84	81	78	80	74.5	72	80	76	54	77	74.5	70
8 inches	83.25	80.5	77.5	79	74.5	71	80	76	54	77	74.5	69.5
12 inches	82.75	80	76.25	78	74.5	71	78.5	75	53	75.5	74.5	69.5
16 inches	81.25	78.25	75.5	76.5	74.5	70.5	78.5	75	53	74.5	74.5	69.5
20 inches	80	77.5	74	75	74.5	69	77.25	74.5	52.5	73.25	74.5	68.75
24 inches	78	76			74.5		77	73.5	51.5	73.25	74.5	68.5
28 inches							77	73.5	51.5	73.25	74.5	68.5
32 inches							76.5	73	50	72.75	74.5	68
36 inches							75	72		72.75	74.5	67
40 inches											74.5	

and the effects of this are frequently shown by higher water temperatures at Station 2 during summer months when air temperature was the same at both stations (Table I). Wide shallow areas are warmed considerably by direct exposure to the sun, but little heat is so gained in the region of Grimes Mill.

Vertical temperature readings were initiated in an attempt to locate spring-fed pools, since the classical idea concerning such pools is that they exhibit a sharp temperature decline near the bottom. In July, 1948, it was decided that both Stations 3 and 4 were spring-fed as they exhibited the vertical temperature patterns shown in Table II. When all surface flow ceased in September of that year, Station 3 soon became uniform in temperature and eventually dried completely in late October. Station 4, on the other hand, maintained the same vertical temperature pattern and fell only slightly below the water level reached when the riffles stopped flowing. These facts led to the belief that Station 3 was either not spring-fed or that subterranean flow ceased at the same time as did that on the riffles. Station 4 was assumed to be spring-fed. When it quickly filled in November, 1948, the stream was uniform in temperature from Station 1 through Station 4. It was later found that temperature would be the same at all stations when water at Station 2 was 17

inches or more in depth. When water fell markedly below this level in the summer of 1949, Station 3 soon exhibited the thermal stratification that had characterized it during the summer of 1948. Studies of its temperature at various depths related to temperatures on Station 2 soon demonstrated that thermal stratification of a pool could result without the agency of subterranean flow. Reference to Table I, which shows the temperature data in simplified forms for the four stations, should indicate manners in which stratification arises. Pools become stratified because differences between their temperature and that of rapids result either in warmer water flowing across the surface or in cooler water flowing along the bottom. A stratification of the first type once formed at Station 3 in the following manner: A summer rain flushed the stream and for a short time thereafter water temperature was lowered and made uniform throughout. As the stream level fell, air temperature rose and in a period of $\frac{1}{2}$ day warmed surface water on pool and riffle above sufficiently to bring about density differences with flow across the top and dead water near the bottom. This type of stratification was present on July 28, Sept. 7, and Sept. 12, 1949, as may be noted in the table. On the last date the pool surface was slightly colder than water in the riffle above.

Stratification of the second type, in which colder water is in motion along the bottom, was more common and was initiated when riffle water dropped to lower temperatures than the pool at night. Since the riffle (Station 2) is more shaded than the pool (Station 3) this condition was frequently maintained during the following day. Such a flow along the bottom left dead water at the top of the pool for most of its length. At times all riffles were of the same temperature and flow was restricted to this water which passed under warmer layers in all pools. On Sept. 23, 1949, water 58° F. was so in motion, and on Nov. 5, 1949, water 44° F. in temperature was making its way down along the bottom. Upon occasion water flowed through Station 4 some distance above the bottom, and then colder water at the bottom may have represented subterranean flow, although this condition could have been due to warming of riffle water farther upstream.

It should be emphasized that thermal stratification of pools in this stream is a phenomenon associated mainly with low stages in summer and fall, although it has been noted during other seasons when tributaries bring colder or warmer water into the stream. Surface temperature is also subject to greater variation during times of low water. During winter and spring months water movement was sufficient to prevent the formation of such density currents. It was not always necessary for depth at Station 2 to be increased to 17 inches to remove old water from the stream, since colder rain water often raised pool levels to a point where warmer water standing above would be floated off. Frequent water level fluctuation would appear to combat the formation of thermal layers. When conditions favor their formation, density layers can exist in very shallow water. Station 3 was usually less than 2 feet in depth and Station 4 less than 3 feet when stratification was most common.

CHEMICAL FEATURES

Oxygen

Relationships of water temperature and quantities of dissolved oxygen were often puzzling since amounts of oxygen were observed to vary both directly and indirectly with temperature (Fig. 9). Inasmuch as indirect ratios between the two are to be expected, it was soon discovered that lowered oxygen concentration in colder weather was due to an increased oxygen demand. Decline of oxygen with temperature decrease was first observed in the fall of 1948, when water was present only in pools which became clogged with fallen leaves and other organic debris near the onset of colder weather. The figure will also indicate that this condition characterized the fall of 1949, when flow was maintained, although reduced. At this time water of both rapids and pools showed considerable oxygen demand, which was attributed to quantities of leaves that almost choked the slow-flowing stream. During winter of 1948-49 oxygen remained fairly constant at 7.5 ml. per l. and later increased to above 8.0 ml. per l. in March, April, May, and June when water was warmer.

An increase in oxygen content with higher stream temperature represents the effect of photosynthesis by benthic algae, which develop rapidly after being almost totally absent during winter. Oxygen content was higher during the winter of 1949-50 than during that of 1948-49, but increased concentrations appeared in the springtime of 1950.

Variation among stations. Although variation was to be expected, an outstanding peculiarity was that water at Station 2 regularly exhibited a higher oxygen concentration than that at Station 1, although water was usually warmer at Station 2. It might appear that sudden increase in amount of surface exposed per volume of water occurring at Station 1 makes for greater absorption of oxygen along with accelerated gain or loss of heat. However, it seems that the increase

in oxygen can be more readily attributed to the photosynthetic action of periphyton algae on the bedrock bottom of the shallow stretches at Station 1 and below. Periphyton growth is considerably reduced in the riffle above Station 1 and would have more effect upon the water below than at Station 1.

Differences in oxygen content at various stations and depths may be noted in Table I. Surface waters of pools normally exhibited slight oxygen demand and less oxygen than those of rapids during middle and low stages. Due to slower rate of flow, but mainly to eddies, pools serve as 'catch basins for certain amounts of organic debris, decomposition of which reduces oxygen supply gained by flow over rapids, where supply is augmented by photosynthesis. Oxygen content usually differed in Stations 3 and 4 in upper and lower layers of water, and lower concentrations at Station 4 appeared to be due to greater quantities of eddy deposited detritus.

Vertical oxygen distribution. Additional oxygen depletion occurred in deeper waters of pools when thermal stratification was of the first type, i.e., flow of warmer water across the top with immobilized cold water near the bottom. In Station 4 diminished oxygen supply was sometimes evident in colder water in motion along the bottom. Oxygen stratification may be correlated with thermal stratification in Table I.

Carbon dioxide

Free carbon dioxide was present only during the fall when water was nearly filled with leaves and other organic debris. At other times production of free CO_2 could be detected only by its influences upon the bicarbonate content. Drop of pH level to slightly above 7.0 during periods of high water was due to tremendous dilution with neutral rainwater and not to free CO_2 production. Carbonic acid was present in the pools that contained water during the fall of 1948, and in both riffles and pools during the fall of

1949. In 1949, however, free CO_2 was less concentrated in riffles than in pools due to its consumption by periphyton. Removal of much free CO_2 by aeration at this time of the year appears unlikely, as there is practically no turbulence.

Half-bound carbon dioxide. As shown by methyl orange alkalinity in Table III and in Figure 9, quantities of bicarbonate in solution were always considerable except during winter months. Concentrations of this substance were frequently greater in surface waters of pools than in those of rapids. With practically no exceptions, greater concentrations of bicarbonate occurred in deeper pool waters than near the surface, indicating decomposition even when bottoms are of bedrock and seemingly quite clean of organic matter, as at Station 3. Since the greatest amounts of decomposable organic matter in pools are found in eddy-deposited silt, sand, and gravel, the abundance of such materials in Station 4 resulted in methyl orange alkalinity that was normally greater than at other stations.

Bound carbon dioxide. Monocarbonate, indicated by phenolphthalein alkalinities in Figure 9 and Table III, occurred in largest quantities in riffle water over the greater part of the year. An increase of phenolphthalein alkalinity on riffles was generally accompanied by a decrease in methyl orange alkalinity, due to the influence of photosynthesis by periphyton algae that removed CO_2 from bicarbonate. When free CO_2 production was at its maximum during the fall, phenolphthalein alkalinity disappeared from riffle water. It was also absent upon occasion during winter months when free CO_2 was not in solution. Phenolphthalein alkalinity was usually higher at Station 2 than at Station 1, another indication of greater growth of benthic algae below than above Station 1. Monocarbonate was present in greatest quantities during early spring when flow was in high or upper middle ranges. During this period of the year strong flow and low temperature combine to prevent decomposition in the

[illegible]

stream, and early algal growths transform much of the bicarbonate into the bound form.

Total carbonate content was usually consistent along the Grimes Mill section on any given date, although methyl orange and phenolphthalein alkalinity (usually) varied from station to station. During warmer seasons monocarbonate formed by photosynthesis on rapids is transformed again to bicarbonate in pools by union with free CO_2 produced there by decomposition. On the rapids below pools CO_2 is again removed from the bicarbonate in solution. Phenolphthalein alkalinity is so increased on rapids and reduced in pools, while the opposite is true for methyl orange alkalinity. Upon occasion (Table III, Sept. 12, 1949) the monocarbonate formed by the action of photosynthesis would leave solution on rapids and so reduce the total carbonate content. On many such occasions the supply was renewed in the pool or pools below by addition of bicarbonate. This fact suggests that monocarbonate in solution normally snaps up free CO_2 as quickly as the latter is formed in pools, and that when quantities of monocarbonate in solution are insufficient to combine with all CO_2 being produced, the carbonic acid will react slightly with the stream bed and increase methyl orange alkalinity. However, there seemed a limit to the amount of limestone available to chemical erosion by carbonic acid, since during the season of greatest decomposition in the stream free CO_2 was present in solution, indicating lack of contact with limestone. Water at the four stations differed but little in total carbonate content on most occasions, demonstrating little erosion of limestone. The stream bed was covered with periphyton and/or ooze during the growing season, either type of coating appearing adequate to keep most limestone from contact with water.

Quantities of mono- and bicarbonate in solution generally varied inversely with rate of flow. It appeared likely that surface runoff and dilution of ground water

were responsible for this condition. When the earth becomes soaked with water during periods of heavy precipitation, additional rain flows along the surface of the ground with little opportunity to pick up bicarbonate, as it comes in contact with very little free CO_2 . The limestone bed in the region of the first four stations is protected from erosive action of carbonic acid by coatings of periphyton and ooze that keep it from contact with water when the acid is present. During periods of great flow the limestone is swept clean of such coverings, but at these times no free CO_2 is present in the water.

Hydrogen ion concentration

In general pH values depended upon the nature (free, half-bound, or bound) and quantities of carbon dioxide in solution. From a high of 8.7 (9.1 in headwaters) in early spring pH decreased to less than 8.5 in late spring and early summer, remaining above 8.0 until the onset of heavy decomposition in the fall, when it dropped to the usual annual low of 7.2-7.3 (Fig. 9 and Table III). During the high water season of late fall and winter, pH remained at 8.0 or slightly above, occasionally falling to slightly above 7.0 when great amounts of rainwater filled the stream. Higher hydrogen ion concentration in early fall reflects maximum decomposition in the stream, while low concentrations in the early spring represent great photosynthetic action of benthic algae. Occasional concentrations of blanketing algae were noted to raise pH to 9.0 or above in smaller streams in summer and fall. Surface waters of pools and rapids normally differed but slightly, since surfaces of pools frequently exhibited chemical alterations that had taken place on the rapids above. Deeper waters of pools were frequently more acid than those near the surface. Station 4 was usually lower in pH than Station 3, at all levels and seasons. Consistent pH values during the greater part of the year denote the well-buffered nature of the water, which remained slightly alkaline even

when considerable quantities of free CO_2 were produced in the fall.

Other chemical features

Iron was present in very slight amounts, varying from 0.4 to 0.8 ppm., with the latter figure prevailing over the greater part of the year. Manganese was present in trace amounts, and chloride varied from 1 to 4 ppm., with greater concentration in summer. Phosphate determinations began in early summer, 1949, and have been carried on to date. At present, understanding of phosphate relationships is rather vague, but the following facts have been disclosed. In the region of the first four stations phosphate was not present during spring and was lacking during middle and low stages of summer, except during and shortly after rises in water level, when it sometimes reached a concentration of 4 ppm. (as PO_4). In smaller divisions of the stream, phosphate was frequently present in trace amounts during decline in water level, but was quickly built up to around 6.0 ppm. when rains added more water to the stream. At the onset of heavy flow in December 1949, phosphate increased suddenly to 8.0 ppm. in the headwaters and to 6.0 ppm. in the region of Grimes Mill but quickly fell to 0.0 and showed no increase during winter and early spring.

Sources of minerals in solution

A stream flowing over solid and broken limestone would be expected to maintain its carbonate content at the expense of its basin. Data accumulated over the 21-month period, of Boone Creek indicate, on the contrary, that only in restricted areas and in relatively small amounts, is limestone from the stream bed brought into solution. This finding was unexpected, but such a conclusion is almost inescapable when one considers that total carbonate concentration was nearly uniform at the four stations on most occasions, and that, during the period of greatest decomposition in the stream, carbon dioxide was able to exist in the free

form. Also significant is the fact that relatively little bicarbonate was added to the water when carbonic acid was in solution. Acid action is evidently of minor importance in erosion of the stream bed in the middle and lower sections.

Sampling of headwater branches and springs has indicated that most of the carbonate present in stream water is brought into solution by water flowing through the earth. Some variation in quantity of minerals in solution occurs among the various springs sampled, but changes undergone by their water after it leaves the earth have so far been the same for all. In the early fall (Oct. 8, 1949), when headwater sampling began, all springs had a pH of 7.6 and methyl orange alkalinity varied from 198 to 203 ppm. At this season decomposition was well under way in the smaller divisions of the stream, and pH of spring water quickly dropped to 7.3 downstream with methyl orange alkalinity remaining unchanged. Free CO_2 varied from 27 to 42 ppm. in the open water. On this date water at Grimes Mill varied in pH from 7.4 to 7.9, and in methyl orange alkalinity from 215 to 217 ppm. Study of Table III will show that photosynthesis was operating to diminish free CO_2 on the riffle below Station 1, with bicarbonate content being unaffected. If the 14 ppm. greater concentration of bicarbonate in the Grimes Mill region represented acid erosion of the stream bed, only a relatively small amount (6.45 per cent) of total carbonate content is to be accounted for in this way. In the fall of 1948 when only isolated pools were present, free CO_2 was more concentrated in their water than in the fall of the following year when flow was maintained. Methyl orange alkalinity in pools reached the same concentration in both years.

During the winter period of increased precipitation and flow, surface runoff of rainwater frequently filled the upper branches, joined with flow from springs, and made analysis of pure ground water impossible. Such dilution greatly low-

ered the mineral content of the stream, but marked variation among different stations was evident even then. During this period (December and January) pH varied from 7.1 to 7.9, methyl orange alkalinity from 58 to 130 ppm., and phenolphthalein alkalinity was totally lacking. No definite pattern was evident, since individual stations, both up- and downstream, varied over the entire ranges given. Variation among stations and at any one station at different times was greater during the period of heavy flow than at any other season.

When the stream level dropped to middle stages for a greater period of time in late February and March, 1950, analysis of springs and upper branches disclosed relationships that were reminiscent of those existing between pools and rapids during middle and low stages of the stream at Grimes Mill. Growths of periphyton occupied most of the bottoms of upland pasture brooks in late February, 1950, and their algal components quickly altered the chemistry of spring water. On March 24, 1950, water just leaving the spring at Station 9 had a pH of 7.3, 7.0 ppm. free CO_2 , 0.0 phenolphthalein alkalinity, and 102 ppm. methyl orange alkalinity. The pool below contained some *Spirogyra*, and the rill below the pool had diatoms covering all sticks and bits of vegetation, and some *Lemanea* on the bottom. Water in this rill, 25 feet below the pool and 50 feet below the spring, exhibited a pH of 8.3, 0.0 free CO_2 , 1.5 ppm. phenolphthalein alkalinity, and 100 ppm. methyl orange alkalinity. Basin Springs on Mar. 31, 1950, had a pH of 7.2, 10 ppm. free CO_2 , 0.0 phenolphthalein alkalinity, and 112 ppm. methyl orange alkalinity. One hundred and fifty feet down the branch these chemical features were altered so that pH was 8.3, free CO_2 0.0, phenolphthalein alkalinity 3.0 ppm., and methyl orange alkalinity 109 ppm. Other springs and their outlets showed similar relationships that differed quantitatively to a minor degree. It was evident that shortly after reaching the surface photosynthesis re-

moved very little of total carbonate but all carbonic acid from ground water. Farther downstream removal of carbonate occurred. The extent of photosynthesis varied in different upland branches and union of two or more with subsequent mixing resulted in water that was chemically quite unlike that supplied by any of the tributaries. Water flowing down any one tributary in springtime evidenced greater effects of photosynthesis with distance. Sometimes the progressive decrease in carbonate content continued after water reached the main creek, and frequently was evident at Station 10. At other times water at Station 10 showed less effects of photosynthesis than that farther up various tributaries. Water in the Grimes Mill section never showed the effects that photosynthesis produced at Station 10 and above. Greater volume of flow, considerably augmented by seepage from the surrounding bluffs, appears to moderate the effects of photosynthesis here.

Phosphate also appears to be brought into solution in ground water that flows into the upper divisions of the stream. Noticeable amounts of this salt appeared in the creek during and shortly after rises in water level. Quantities in solution declined in each instance with water level, disappearing from middle and lower reaches, and dwindling to trace amounts in the uppermost branches. Following increases in flow during late summer and early fall, phosphate had its greatest concentrations in upstream waters and exhibited uniform diminution with distance down the stream, being 6.0 to 7.0 ppm. at Stations 6, 7, 8, and 9, 4.0 ppm. at Station 10, and 3.0 ppm. in the Grimes Mill section. This pattern of decline, plus the fact that it was present in trace amounts in small pasture brooks during the low water season, indicates its addition to the water in the upper sections. When supply diminishes with decreasing flow, its consumption becomes almost complete in the headwater branches. At the onset of heavy flow in December 1949,

phosphate entered solution in quantities up to 6.0 ppm., but soon disappeared, except for occasional trace amounts in up-permost sections.

Phosphate in the stream may owe its origin partially to manure and fertilizer, but a more likely source is calcium di-phosphate rock that occurs on the surface and in upper layers of the soil in many of the headwater pastures. This rock is insoluble in water but can be eroded by carbonic acid, and, if coming from the rock, phosphate, like carbonate, owes its presence in the stream to the action of free CO_2 . Phosphate occurred in spring water only for short periods of time following rains. This fact indicates that it is added to water only by flow through upper layers of soil, since during drier seasons, water passes through top layers only during and shortly after rains. Water flowing from springs comes from deeper regions of the earth, but, following rains, the flow through surface layers may discharge through the same opening. Loss of phosphate with continued high rate of flow during winter rainy periods seemingly represented dilution and exhaustion of carbonic acid in the soil.

Seasonal chemical variation

Variation of surface waters at the first four stations over the seasons is shown in Figure 9. As brought out in the above account, the chemical features studied are affected mainly by decomposition and photosynthesis, and the quantitative effects of each or both of these factors are to a large degree controlled by the volume of water moving down the stream. Decomposition and photosynthesis tend to moderate the influences of each other. In the early spring when waters are too cold to permit noticeable decay of organic materials, photosynthetic activity of bottom algae normally has its greatest effect. Decomposition, which often neutralizes the influence of photosynthesis, has its heyday in the fall. Both processes exert their greatest influences when volume of flow is in middle and low ranges. The

effects of water level changes, temperature, photosynthesis, and decomposition upon the four major chemical features may be gained by study of Figure 9 and need no detailed description here. In general it may be said that phenolphthalein alkalinity reflects the photosynthetic process and that methyl orange alkalinity owes its existence to decomposition, either in the stream or underground. Oxygen and pH levels depend upon the outcome of the struggle between these two mutually counteracting forces. Figure 9 presents mean values for surface waters, which are not too indicative of individual variation among pools and rapids, and, of course, do not take into account chemical features at greater depth in pools.

DISCUSSION

As mentioned in the introduction, there is little previous work known to the author that deals with physical and chemical factors in streams in sufficient detail to permit much comparison with the data obtained in this investigation. Pennak (1943) found carbonate to be less concentrated during low stream stages, although considerable variation occurred that was not explained. In his section on running waters in general, Welch (1935) deals with broad aspects of stream limnology, which represented the major effects of investigators to that date. Butcher, Pentelov, and Woodley (1930) noted the influence of photosynthesis upon oxygen supply in streams, as they found highest oxygen concentrations during the day and lowest amounts in solution during the night. Muttkowski (1929) states that constant churning and mixing due to current in streams does not permit a thermal stratification. Cowles and Schwitalia (1923) found pH to be higher in rapids than in pools of a small seepage stream in Maryland, and attributed this difference to removal of free CO_2 by aeration. Stehr and Branson (1938) found oxygen content higher in riffles than in pools, and more concentrated in spring than in sum-

mer in an intermittent stream. Powers (1929) reported a gradual increase in pH with distance down a trout stream in the Great Smokies. He assumed the difference was due to aeration, since he could produce it by shaking upstream samples in a test tube. Berg (1943) reports thermal stratification in the Susaa (Denmark), but only in meanders where flow is very slow and water deep. Oxygen also exhibited stratification in the meanders but not in the headwaters. Berg also noted that phosphate was higher in summer than in winter, and believed that its presence in ground water indicated addition of animal or human waste products. Highest phosphate concentration in waters of the Susaa was 1.8 ppm.

In describing certain limnological features of a stream it appears to be of fundamental importance to specify the normal or most frequent state of the stream with regard to conditions relating to rate of flow. The distinction between pool and riffle is one that may be recognized only when the water level is below a definite point, since any stream will form a rushing torrent in which no such divisions may be seen when water levels are extremely high. Also, when water levels are low, pools with quiet water appear in what was previously flowing water on rapids. Therefore, it seems that the best classification of a stream is one that is descriptive of the usual condition with regard to rate of flow over the greater part of the year. Streams are much divided into pools and rapids near the headwaters, and smoothly flowing areas tend to occupy more and more space with distance down the stream until all divisions disappear in a fairly smooth flowing layer in the larger rivers. Hence, the greater the rate of flow, whether due to greater area drained or greater precipitation, the less frequent the separation into pools and riffles, and vice versa.

A headwater stream, such as Boone Creek, consists of alternating pools and riffles for the greater part of the year, with only infrequent periods in which heavy

precipitation wipes out all such distinctions. A creek of this sort offers an environment that varies from rapid to pool, in different rapids, and in different pools. Major causes for such differences lie in various features of the stream bed that affect velocity of flow and current patterns, and the character of the immediate surroundings which determine exposure to sun and wind. Development of certain elements of the biota may markedly affect the water, but such a growth depends upon a suitable combination of factors mentioned in the preceding sentence.

Relations of rapids and pools

A pool offers an environment that differs from that of a rapids chemically, as well as in current intensity, temperature, depth, light, etc. Since pools alone permit any noticeable decomposition and free CO_2 production in the stream during the greater part of summer and fall, their presence permits maintenance of constant quantities of bicarbonate in solution. Without pools, reduction of bicarbonate by photosynthesis on rapids would generally result in smaller and smaller quantities of available CO_2 with distance downstream, bringing a reduction in algal growth in the lower reaches. The state of affairs present in early spring in upper regions would then continue throughout the stream and growing season. However, this is prevented by events occurring in pools, which make for greater growth of basic food organisms in periphyton on riffles. Formation of pools is very important in the interest of total biological productivity, even if their only function in this respect is to serve as catch basins for decomposable organic debris. Due to their algal growth, riffles are sites of development of the majority of basic food organisms in this stream. Periphyton elements here depend upon bicarbonate as their chief source of CO_2 during the greater part of the year; but, during the short period of great free CO_2 production in the fall, they utilize the gas in solution, frequently re-

moving large quantities and altering pH as well.

Spring-fed pools

Studies on Boone Creek have to date produced little information that will permit recognition of spring-fed pools when the stream is flowing. They may be recognized by the persistence of thermal and chemical stratification after surface flow has ceased in the stream, but drying to isolated pools is a rare phenomenon. Normally, decline in temperature with depth can occur in any pool as a result of differences in temperature in the pool and rapids above. When thermal differences are present, riffle water may flow across the pool on the surface, along the bottom, or at any intermediate depth. Colder immobilized water at the bottom of a pool could possibly represent direct entrance of ground water, but it could also be due to warming of the riffle above, leaving colder water at the bottom. Water temperature can serve as no reliable guide in locating entrance of subterranean flow not visible at the surface in a flowing stream.

The chemical features of spring-fed pools likewise differ but little from those of ordinary pools. Oxygen decline with depth occurred in all pools under certain conditions already described. Analysis of spring water in the upper regions of the stream demonstrated that oxygen is less concentrated in water just leaving the earth than in that in the stream or farther down the riffle from the spring. However, oxygen supply in spring water is not notably deficient, since it averages around 8 ml. per l. in the spring and around 5-6 ml. per l. in the fall, when it is even lower (3 ml. per l.) in the stream. At any time of the year oxygen present in ground water differs insufficiently from that of the stream to permit distinction between ground water and colder stream water immobilized near the pool bottom, as the latter frequently exhibits less oxygen than surface water. During autumn, when oxygen content of stream water is lower

than that of ground water, quantities in the latter are quickly reduced when it reaches the stream and contacts decomposition products.

Ground water normally contains some carbonic acid when it leaves the earth, and carbonate only in the half-bound form. However, upon many occasions the total carbonate content of spring water and that of the stream are almost identical, although both phenolphthalein and methyl orange alkalinity are present in the latter. The pattern of bicarbonate consumption and replenishment in rapids and pools described above quickly removes any distinctions by which ground water might be recognized. The rapidity with which ground water assumes the same chemical characteristics as those of the stream is continually demonstrated at Station 10, where two small springs discharge into the creek at the bottom of the left bank. On Mar. 24, 1950, for example, water from these springs had a pH of 7.3, 7.0 ppm. free CO_2 , 0.0 phenolphthalein alkalinity, 143 ppm. methyl orange alkalinity, and 7.4 ml. per l. oxygen. Water in the stream above and two feet below the entrance of the springs had a pH of 8.0, 0.0 free CO_2 , 11.0 phenolphthalein alkalinity, 95 ppm. methyl orange alkalinity, and 10.1 ml. per l. oxygen. Flow from these springs amounted to approximately 100 cubic feet per hour on this date, but their water was lost as soon as it joined the much greater flow in the stream. This same phenomenon, occurring when subterranean water enters the stream below the surface of a pool, probably accounts for its lack of influence upon the water chemistry of the pool during periods of active flow. Flow of ground water becomes less during periods of low precipitation bringing about less flow down the stream, but probably maintaining volume relationships between water passing down the stream and that entering directly from a spring. Thus a spring has little opportunity to influence either the temperature or chemistry of a pool until flow down the stream has stopped. After stream flow

has ceased, the spring furnishes the only water entering the pool, and, since this ground water is colder than that of the pool, temperature decline with depth is maintained. Chemical stratification similar to that observed in many pools when flow was present is also retained. Non-spring-fed pools become uniform in both temperature and chemistry and show decrease in water level. Detection of spring-fed pools in a flowing stream appears unlikely when springs enter below the surface, even if thermal and chemical studies are continued over an extended period of time, unless, possibly, they are run almost hourly over a period of a few days.

Individuality of pools and rapids is a marked characteristic during middle and low stages of the stream. Most factors contributing toward variation then have more effect upon the stream, since the volume of water they affect occupies a larger and larger percentage of total flow as the stream level falls. In upper regions of the stream, percentage of total volume affected is very great except during extreme high flow. Individuality of pools and rapids reflects variation in stream bed and surroundings, such as increase and decrease in width and depth of stream bed, difference in amount of exposure, obstructions to flow, and construction of the bottom. Obstructions and non-uniform width of stream bed affect current patterns and induce great deposition of organic and other materials by eddies in some spots and little or no deposition in others. Degree of exposure largely determines the extent of algal development, which, in turn, influences water chemistry. Pools may differ in chemistry and certain physical features because of distinct differences in themselves, but the nature of surface water in a pool is often largely due to processes occurring in the rapids above. Similarly, water in rapids may be influenced by events in pools above. It thus appears that features that make a riffle or pool distinct from its fellows also may operate to make the pool or rapids below stand out in its group.

Factors causing differences among rapids are: (1) variation in amount of surface exposed per volume, which mainly affects water temperature; (2) degree of exposure, which limits algal growth and affects temperature; (3) nature of the bottom, whether broken or solid rock; and (4) the character of the pool or stretch of water above. Individuality of pools is largely determined by: (1) events occurring in the riffle above; (2) the extent of organic deposit in the pool, which itself is largely determined by current patterns; (3) depth and area; and (4) degree of exposure. When the stream ceases to flow, difference among pools left are largely due to the presence of subterranean flow from banks in some and not in others. How these various factors induce variation in rapids and pools has been brought out in the above account and need not be repeated here.

Differences noted between upper and lower regions of the stream are mainly due to the greater volume of water downstream. As flow decreases, the downstream riffles are more influenced by photosynthesis, as the water it affects represents a larger percentage of the total. Greater volume of flow has a moderating effect upon photosynthesis and other processes and tends to make more uniform chemical and physical features over greater lengths of stream. During a great part of the year volume of flow is insufficient to mask the influences of various modifiers in Boone Creek, and since their effects are operative during a major part of the growing season, their influences on productivity in a stream of this size and type are considerable.

SUMMARY

1. Change in rate of flow is more accurately represented by water level change on rapids, since various obstructions to flow in pools bring about greater rise or fall when conditions favor eddy formation.

2. Surface water temperatures are

largely determined by those of the air, but exposure of more surface per volume in wide shallow areas of the stream results in water temperatures more nearly like those of the air. Thermal stratification is present in pools during summer and early fall, seasons of slowly declining water levels.

3. Oxygen content of stream water is greatly influenced by photosynthesis of benthic algae throughout the growing season. Highest oxygen values, due to photosynthesis, occur in the spring with rising temperature and the lowest, due to decomposition, in the fall with falling water temperature. Oxygen stratification occurs with thermal stratification of pools.

4. Free CO_2 is present in the open stream only during a brief period in early autumn. Half-bound CO_2 reaches its greatest concentration during autumn, but bound CO_2 is present in largest amounts in early spring. The greatest percentage of carbonate in solution is present when ground water flows from springs, and very little is added by the action of carbonic acid upon the limestone stream bed, due to protective coatings of periphyton and ooze. Hydrogen ion concentration is greatest in fall and least in spring. Phosphate was present in stream water for brief periods following rises in water level during summer and fall, and resulted from flow through soil in the upper stream regions. Seasonal chemical variations reflect the influence of photosynthesis, decomposition, variation in rate of flow, surface runoff, and rate of algal growth.

5. Spring-fed pools are very difficult if not impossible to detect in a flowing stream.

6. Greater volume of flow in downstream regions obscures the effects of various physical and chemical modifiers, and knowledge of these is best gained by study of smaller headwaters during periods of high water or by analyses of water in lower regions at times of low water levels.

7. Major consumption of nutrient minerals occurs on rapids, but events occur-

ing in pools serve to maintain supplies of CO_2 available to photosynthesis.

LITERATURE CITED

- Allen, W. R. 1945. Wildlife and outdoor Kentucky; in: Beers, H. W. (ed.). Kentucky: designs for her future. Lexington: Univ. Kentucky Press. Chap. 6: 102-130.
- Allen, W. R., and M. E. Clark. 1943. Bottom-preferences of fishes of northeastern Kentucky streams. Trans. Ky. Acad. Sci., 11 (2): 26-30.
- American Public Health Association. 1936. Standard methods for the examination of water and sewage. 8th ed. New York.
- Behning, A. 1927. Das Leben der Wolga, zugleich eine Einfuhrung in die Flussbiologie. Die Binnengewasser, vol. 5, 168 pp. Stuttgart: Erwin Naegele.
- Berg, Kaj. 1943. Physiographical studies on the River Susaa. Folia Limnologica Scandinavica, 1: 174 pp.
- . 1948. Biological studies on the River Susaa. Folia Limnologica Scandinavica, 4: 318 pp.
- Butcher, R. W., F. T. K. Pentelow and J. W. A. Woodley. 1930. Variations in composition of river waters. Int. Rev. ges. Hydrobiol. Hydrogr., 24: 47-80.
- Call, R. E. 1896. Fishes and shells of the Falls of the Ohio. Memorial History of Louisville, 1: 9-20.
- Clarke, F. W. 1924. The composition of the river and lake waters of the United States. U. S. Geol. Sur., Prof. Paper, no. 135. 199 pp.
- Clench, W. J., and Henry van der Schalie. 1944. Note on Naiades from the Green, Salt, and Tradewater Rivers in Kentucky. Pap. Mich. Acad. Sci., Arts, & Lett., 29: 223-228.
- Cowles, R. P., and A. M. Schwitalia. 1923. The hydrogen ion concentration of a creek, its waterfall, swamp and ponds. Ecology, 4: 402-416.
- Danglade, Ernest. 1922. The Kentucky River and its mussel resources. U. S. Bur. Fish., Doc. 934. 8 pp., fig. 1-7.
- Evermann, B. W. 1902. Description of a new species of shad (*Alosa ohioensis*) with notes on other food fishes of the Ohio River. Rept. U. S. Fish. Comm., 1901: 273-288, 6 fig.
- . 1918. The fishes of Kentucky and Tennessee: a distributional catalogue of the known species. Bull. U. S. Bur. Fish., 35: 295-368.
- Galtsoff, P. S. 1924. Limnological observations in the upper Mississippi, 1921. Bull. U. S. Bur. Fish., 39: 347-438.

- Garman, Harrison.** 1894. A preliminary list of the vertebrate animals of Kentucky. *Bull. Essex Inst.*, **26**: 1-63.
- Howland, J. W.** 1931. Studies on the Kentucky black bass, *Micropterus pseudaplites* Hubbs. *Trans. Amer. Fish. Soc.*, **61**: 88-94.
- Hubbs, Carl L.** 1927. *Micropterus pseudaplites*, a new species of black bass. *Occ. Pap. Mus. Zool., Univ. Mich.*, no. 184. 15 pp., pl. i-ii.
- Jordan, D. S., and Joseph Swain.** 1883. List of fishes collected in the Clear Fork of the Cumberland, Whitley Co., Ky., with descriptions of three new species. *Proc. U. S. Nat. Mus.*, **6**: 248-251.
- and **A. W. Brayton.** 1877. A partial synopsis of the fishes of Upper Georgia, with supplementary papers on fishes of Tennessee, Kentucky, and Indiana. *Annals N. Y. Lyc. Nat. Hist.*, **11**: 307-377.
- Kirsch, P. H.** 1892. Notes on the streams and fishes of Clinton Co., Kentucky, with a description of a new darter. *Bull. U. S. Fish Comm.*, **10**: 289-292.
- . 1893. Notes on a collection of fishes from the southern tributaries of the Cumberland River in Kentucky and Tennessee. *Bull. U. S. Fish. Comm.*, **11**: 257-268.
- Kirtland, J. P.** 1841. Descriptions of the fishes of the Ohio River and its tributaries. *Boston Jour. Nat. Hist.*, **3**: 338-352, 369-382, pl. iv-vi, xxvii-xxix.
- . 1845. Descriptions of the fishes of the Ohio River and its tributaries. *Boston Jour. Nat. Hist.*, **5**: 21-32, pl. vii-viii.
- Kofoed, C. A.** 1900. The plankton of Echo River, Mammoth Cave. *Trans. Amer. Micr. Soc.*, **21**: 113-126.
- . 1903. Plankton of the Illinois River. *Bull. Ill. Nat. Hist. Sur.*, **6**: 95-629.
- . 1908. Plankton of the Illinois River. *Bull. Ill. Nat. Hist. Sur.*, **8**: 1-360.
- Muttikowski, R. A.** 1929. The ecology of trout streams in Yellowstone National Park. *Roosevelt Wildlife Annals*, **2**: 155-240.
- Neel, J. K.** 1938. Lower Howard's Creek: a biological survey. Unpublished master's thesis.
- Ortmann, A. E.** 1926. The Naiades of the Green River drainage in Kentucky. *Ann. Carnegie Mus.*, **17** (1): 167-188.
- Pennak, R. W.** 1943. Limnological variables in a Colorado mountain stream. *Amer. Midl. Nat.*, **29**: 186-199.
- Powers, E. B.** 1929. Fresh-water studies. I. The relative temperature, oxygen content, alkali reserve, the carbon dioxide tension and pH of the waters of certain mountain streams at different altitudes in the Smoky Mountain National Park. *Ecology* **10**: 97-111.
- Putnam, F.** 1872. The blind fishes of Mammoth Cave and their allies. *Amer. Nat.*, **6** (1): 6-30, pl. i-ii.
- Rafinesque, Constantine.** 1820. *Ichthyologia Ohiensis*. Lexington, Ky. (Reprinted, ed. R. E. Call.)
- Richardson, R. E.** 1921. The small bottom and shore fauna of the middle and lower Illinois River and its connecting lakes, Chillicothe to Grafton: its valuation; its sources of food supply; and its relation to the fishery. *Bull. Ill. Nat. Hist. Sur.*, **13**: 363-522.
- Smith, W. L.** 1942. A study of the food habits of fishes found in limestone streams of Kentucky. Unpublished master's thesis.
- Steher, Wm. C., and J. W. Branson.** 1938. An ecological study of an intermittent stream. *Ecology*, **19**: 294-310.
- Steinmann, Paul.** 1907. *Die Tierwelt der Gebirgsbäche. Eine faunistisch-biologische Studie.* *Ann. Biol. Lac.*, **2**: 1-37.
- Thienemann, A.** 1912. *Der Bergbach des Sauerlandes.* *Int. Rev. Hydrobiol. Hydrogr., Biol. Suppl.*, **4**: 1-125.
- Welch, P. S.** 1935. *Limnology.* xiv + 471 pp. New York: McGraw-Hill.
- Welter, W. A.** 1938. A list of the fishes of the Licking River drainage in eastern Kentucky. *Copeia*, **1938** (2): 65-68.
- Wilson, C. B., and H. W. Clark.** 1912. Mussel beds of the Cumberland River in 1911. *U. S. Bur. Fish., Economic Cir.* **1**. 4 pp.
- . 1914. The mussels of the Cumberland River and its tributaries. *U. S. Bur. Fish., Doc.* 781. 63 pp.
- Woolman, A. J.** 1892. Report of an examination of the rivers of Kentucky, with lists of the fishes obtained. *Bull. U. S. Fish. Comm.*, **10**: 249-288.
- Young, O. W.** 1945. A limnological investigation of periphyton in Douglas Lake, Michigan. *Trans. Amer. Micros. Soc.*, **64**: 1-20.

A FUNCTIONAL, FACTORIAL APPROACH TO PLANT ECOLOGY

JACK MAJOR

Division of Soils, University of California, Berkeley 4

Plant ecology is concerned with interrelations of plants and their environments. This paper proposes a scheme for considering the qualitative aspects of these interrelations with some rigor and completeness. It also makes such interrelations amenable to quantitative treatment.

The proposed scheme is based on the theory that specific environmental factors exist and that they determine the characteristics of vegetation. This theory, implicit in plant ecological literature, can be elaborated to explain some of the empirically determined propositions and concepts of plant ecology.

The concept "interrelations" used by ecologists can be interpreted as the concept "function" used in quantitative science. The two ideas are basically one. Therefore, this paper approaches plant ecology as the study of the mathematical functions which relate vegetation to its environment. More precisely, these mathematical functions relate the specific properties or characteristics of vegetation to the groups of factors which we conveniently call "vegetation determining factors."

The methods and scheme suggested here may appear to contradict the holocoenotic belief exemplified by Cain's (1944:19) statement: ". . . the complex interrelations among the environmental factors, and between them and the organism, with its complex physiological and morphological interrelations, are such as to defy solution in exact terms of causation. Ecological problems not only may be difficult of solution because of the interaction of factors and responses, but they may really be insoluble in a mathematical sense." However, the approach proposed here stresses only that the establishment of quantita-

tative functional interrelations in plant ecology is possible, provided one restricts the study to causation between vegetation and environmental factors (groups of factors determining vegetation) and deliberately omits the causes of variations in the environmental factors themselves. Causes of variations in the environmental factors are considered to be parts of such sciences as climatology, geology, geomorphology, pedology, anthropology, human history, organic evolution, and historical plant geography; they are left outside this treatment of plant ecology. In an etymological sense these sciences are ecological, but they are not considered plant ecology—which is the subject of this paper.

Solution of quantitative interrelations of vegetation and environment can be developed along the line Jenny (1930, 1941, 1946) used for the examination of soils in relation to environment. The basic thought of this paper and many specific ideas in it stem directly from the approach to soils used by Jenny. The writer very gratefully acknowledges this primary debt, the active encouragement Dr. Jenny has given to expansion of his own ideas, and his help on this manuscript. Discussions among Drs. H. Jenny, R. L. Crocker, and N. C. W. Beadle in 1949, which considered some of this paper's points, were attended briefly by the writer who appropriated the mutual conclusion identifying the flora as the independent aspect of the plant cover; vegetation as its dependent aspect. I wish to thank all three men for criticisms and opportunity for discussion. However, they should not be blamed for the following presentation, and it is not implied that they agree with it.

THE FACTORIAL EQUATION

Jenny (1941) relates any soil property, s , to the factors of soil formation as follows:

$$s = f(cl, p, r, o, t). \quad (1)$$

This simply states in abbreviated form that a soil property s is a function of, f , or conditioned by, the five groups of factors represented by the symbols in parentheses. The factors were given these meanings by Jenny:

cl = air climate (regional climate)

p = parent material from which the soil originated

r = topography or relief; referring to slope, exposure, and certain ground water conditions

o = biota or organisms

t = duration of soil formation or time.

These five soil forming factors are evidently the same factors which determine vegetation. . . . This statement is the crux of our argument. A wealth of plant geographical observation has demonstrated that vegetation is distributed in accordance with regional climatic patterns, changes as soil parent material changes, differs on opposing slopes, varies with the geographical differences between floras, and develops with time. The reader is referred for documentation to the classical works by Schimper, Warming, Clements, and to the texts by Weaver and Clements, Braun-Blanquet, Lundegårdh, Oosting, Daubenmire. Most of these books demonstrate in more or less explicit form by their organization the groups of habitat factors on which vegetation depends.

Since the five groups of factors of soil formation are the same factors which condition vegetation, it is permissible to write:

$$v = f(cl, p, r, o, t), \quad (2)$$

where v represents any property of vegetation that can be expressed in quantitative terms, such as weight per unit area.

Jenny designates the factors cl , p , r , o , and t the independent variables, in the mathematical sense. This designation

has caused confusion since, as is well known, some of these factors are not always independent of each other. What Jenny implies is that they may be found in nature under such a great variety of combinations that the effects of one of them on soil can be studied independently of variations among the others.

For example, a given type of rock, say granite, occurs in various climates; thus climate may be considered independent of rock type in its effects on vegetation and soil. Different slopes may be made of one type of rock; thus slope angle may be independent of the geological substratum in its effects. Low or high rainfall may occur in different areas along a given isotherm; therefore, it is possible to evaluate the influence of variable moisture on soil and vegetation at the same mean annual temperature. In other words, among the many different combinations of particular values of cl , p , r , o , and t found in nature it is often possible to select suitable combinations to evaluate the factorial equation. Illustrations of the method are given in subsequent pages.

Not only are specific properties of vegetation, v , related to the five environmental factors, but also entire plant communities, V , are conditioned in the same way. Therefore:

$$V = f(cl, p, r, o, t). \quad (3)$$

A plant community, designated by V and defined as a distinctive organized grouping of the plants living together in a circumscribed area, is a unit of vegetation. Such units have usually been described physiognomically or floristically. Both methods are qualitative, not quantitative, and do not produce a singular, characterizing number. A plant community is usually not summed up in a single number. Therefore, the functional relation of a plant community to its environment cannot yet be described quantitatively, mathematically. However, the dependence of a plant community on its five factors

can be stated in a factorial, qualitative way.

Besides being the factors of soil formation and the factors determining vegetation, these five—climate, soil parent material, topography or relief, organisms, and time—seem also to be factors which fix the character of any ecosystem or geographic landscape. Therefore they may be called ecosystem or landscape factors. They have areal extent and within this area form a unit which has been variously named an ecosystem (Tansley 1935: 299), coenose, biogeocoenose (Sukachev 1944), landscape, natural area (Cain 1947), environment, habitat (Munns 1950: 41), site (Munns 1950: 75) (note that these last three terms *do* include organisms found on the locality considered). None of these terms has prescribed limits of areal extent; and since, with the exception of parent material, there are few sharp breaks in the environmental factors, but instead they vary continuously, the size and extent of the kind of unit geographical area considered here is determined by the purpose and methods of a study.

The equation, $V = f(cl, p, r, o, t)$, has been printed by Tüxen (1931/32: 183) in abbreviated form.¹ Its use is implicit in ecological work at least from Schimper's time to the present. This paper proposes it as one explicit, fundamental, and logical starting point in relating a plant community to its environment. The equation may provide a unified and complete approach to plant ecology, obviously not to plant sociology since the latter's aims are different. Posing the equation is only a beginning.

¹ Tüxen (*loc. cit.*) actually wrote, "Vegetation = f (Climate, Soil, Man), in which simplified scheme the rock, relief, and moisture which are of first importance for soil formation are reckoned to the factor soil and on the other hand the influence of animals in addition to man (in long-cultivated lands at least) may be neglected as vanishingly small. In one large geographic area, natural and climatically uniform, . . . vegetation = f (Soil)."

DEFINITIONS OF TERMS OF THE EQUATION

A principal value of the fundamental equation is in pointing out the need for and in helping to define terms and concepts which are basic to plant ecology. The six concepts represented by the symbols V and v , cl , p , r , o , and t enter the fundamental equation and must be defined.

In accord with equations (2) and (3) in our definitions vegetation itself is dependent; it is dependent on the factors that determine it. A particular plant community is selected from the available flora by the environment of a particular locale, to paraphrase Crocker and Wood (1947), who refer the basic idea to Darwin. The other terms of the equations—the vegetation determining variables—are controlling and are treated as independent factors; that is, each environmental factor is defined so it is independent of the other terms of the equations. Actually, these determining factors are groups of variables classed under the headings climate, relief, etc., as a matter of convenience and logic. The following definitions may be bases for discussion.

Properties of vegetation

Vegetation is defined here as the more or less organized plant cover of a region. It has many definable and measurable properties.

The following v -properties of vegetation can be quantitatively expressed, are therefore suitable for functional relationships, and will illustrate what is meant by a dependent property of vegetation: Autecological (referring to individual plants or plant species) properties include abundance, cover, production or weight per unit area, frequency, site index, constants of the age class distribution curve. Synecological (plant community) properties include abundance, cover of both living and dead vegetation, production or weight per

unit area, constancy, proportions of life forms, number of species in the community, properties of the microclimate (see below) such as relative light values.

The factor climate

Elements of climate are usually listed as amount, kind and periodicity of precipitation, range of temperature, mean temperature, humidity, wind, cloudiness, duration and quality of light, etc. Thornthwaite (1948) has pointed out that climate fundamentally consists of a heat and a moisture factor. Numerical indices of these two factors, including indices of their seasonal distribution, may suffice to classify most regional climates as they influence vegetation.

For purposes of this paper's argument the climate of any site at a given time may be considered as existing on several different levels of relative area. Most extensive is regional climate; local or topographic climates are found within a regional climate; and microclimates or phytoclimates occur within plant cover types.

The regional climate, *cl* of the equations, is defined here as the "standard condition" which the weather station net measures. Regional climate is a spatial and temporal average over an area. According to our basic formulation, regional climate within this area is not a function of the environment operative within the area. Thus regional climate is by definition independent of relief, soil parent material, organisms, and time. This is evidently a pragmatic, convenient definition only. Deviations from the regional climate are here named topographic and phytoclimates, corresponding to the conventional and poorly defined terms local and microclimates.

The local (or topographic) climate is defined as topographically determined. Frost pockets and insolation differences between north and south facing slopes are examples. Since this level of climate

is not usually measured directly but is a function of topography, which is an independent variable determining vegetation, topographic climate is discussed under topography. Such discussion is not intended to minimize its importance.

The microclimate we define as a function of the vegetation, including lack of vegetation, on the site. This level has usually been identified with the plant climate, phytoclimate. Microclimate is, therefore, a strictly dependent variable. As such it may be treated as a property of vegetation. Variations in the vegetative cover are accompanied by variations in microclimates. Thus, microclimate may be considered just as is vegetation a function of the independent variables regional climate (as defined above), soil parent material, relief or topography, biota, and time. Microclimate is not defined here as the climate at an arbitrary small height above the ground. This height depends on the kind of vegetation. Inside a forest the light, air movement, etc., are conditioned by the tall tree canopy; in a grassland the absolute height of vegetation which influences climate is only a few decimeters—but both modifications of the regional climate are defined as microclimate in this paper since both modifications are dependent on vegetation.

Essentially, then, climate as an independent variable is regional climate. Regional climate is to be contrasted with microclimate which is a dependent variable.

The factor soil parent material

Jenny (1941) devotes a number of pages to the question, "What is soil parent material?" The answer is not simple. It is by no means certain that the part of the regolith underlying the soil is that soil's parent material. Jenny mentions pseudoprofiles whose horizontal differentiation is a result of geological stratification and not of soil genesis.

Indeed, Whiteside and Marshall (1944: 14) point out, "Soil parent materials have seldom, if ever, been adequately defined." Adequate definition must include "chemical composition, mineralogical constitution, texture, and structure of the rock" (Jenny 1941: 56). For functional purposes the properties of the soil parent material should have quantitative, single-value statement. This is often difficult.

In short, Jenny's (1941: 52) definition of the soil parent material as the state of the soil system at soil formation time zero will be used here. The properties mentioned, then, are those of the parent rock or geological deposit at the beginning of soil formation.

The factor relief

Topography or relief has several independent aspects: those depths to ground water which are not conditioned by vegetative succession or soil formation; slope properties as degree, shape, length, and direction or exposure; and duration and depth of snow cover not conditioned by plant succession. These are independent variables and are quantitatively measurable.

But slope angle itself may not always be a factor entirely independent of vegetation. Slope, soil, and vegetation in parts of southern Idaho (Bailey 1939) are said to have all developed concurrently, for the slopes now are too steep to stand without a vegetative cover. These slopes are now steeper than the angle of repose of the unconsolidated rock at present found in their profiles. Present slope is dependent on present vegetation and soil. However, slope angle of repose as ordinarily defined by geologists (Van Burkalow 1945) is entirely independent of vegetation. We can accept the geologists' definition and say degree of slope is defined as of zero time of plant succession and soil formation. In this sense degree of slope is an independent variable.

The factor organisms

Organisms may be classified as flora, fauna, and microorganisms. The flora factor is designated o_f , the fauna factor o_a , the civilized man part of the fauna factor o_h , and the microorganisms factor o_m .

Flora factor.—The plant cover has both independent and dependent aspects. The plant cover is both a cause and an effect. We need a way to logically separate the two aspects since habitually causes are considered as independent factors and effects as dependent.

Classically the dependent aspects of the plant cover have been called "vegetation." Vegetation is dependent on the environmental factors. But the flora is not necessarily dependent on specific environmental factors. Depending on a landscape's history one of several different floras could occur there. That is, two regions with the same climate, soil parent material, relief, and time of plant succession may have two different floras. The flora behaves as an independent variable, independent of cl , p , r , t of a given ecosystem. Therefore, in this paper the flora will be considered as one of the independent conditioning factors which determine vegetation.

By flora is meant the totality of plant species present in an area. A floral list is, as Jenny (1941: 203) pointed out, a good first approximation to the plant biotic factor operative in a given area.

Most plant species are effective in conditioning the vegetation of an area only if they produce disseminules and disperse them. Although a plant may be a member of the flora, if it cannot spread and reproduce, it can have no effect on vegetation beyond its own immediate, established periphery. Long-lived plants may be relicts which take no active, dynamic part in a plant community but merely exist passively, without reproducing. Therefore, the flora factor is defined here as the summation of different kinds of viable plant dis-

seminules reaching the area in question.

While historical plant geography, or floristics, tells us what species occur in an area—what its flora is, the autecological peculiarities of each species determine its disseminule production (Salisbury 1942) and dispersal capacity. Thus, both historical plant geography and autecology define the totality of plant disseminules present.

Fauna factor.—The fauna, as a species list, may be independent of the environmental factors. But some aspects of animal populations are not independent. Animal nutrition is notably dependent on the plant cover. Pocket gophers seem to be more abundant in overgrazed mountain meadows (Hall 1946: 444). Seral communities in general may be more densely populated by rodents and some insects than climax communities. Such quantitative characteristics would seem to be dependent features of rodents. Accordingly, as with plant life we shall differentiate the animal life of an area into dependent and independent (fauna) factors.

Human factor.—Civilized man is the most important independent animal factor influencing vegetation. We would include primitive man under o_s . Where, as in the history of Europe, there has been no sharp temporal boundary between primitive and civilized man, such a distinction may not be valid. But the contrast in America between Indian and white cultures is probably sufficiently great. We have, unfortunately, only limited data on the use of fire by American Indians. As to modern man, by cutting of forests, grazing domestic livestock, and controlling predators of wildlife he has changed even wildland landscapes. As animals independent of cl , o , r , p , and t , men may have cattle or sheep graze an area, may have them graze heavily or lightly, and may even change the flora by plant introductions—range reseeding of exotics for example.

Applied plant ecology is concerned with the effects of the factor o_h on

vegetation. When o_h equals zero, we shall define the vegetation as natural. For applied plant ecology the study of natural vegetation would seemingly form the necessary prior basis.

Microorganisms factor.—Microorganisms living in the soil influence soil formation and soil properties. Through these activities they also influence the vegetation growing on the site. Therefore, conclusions on the functional nature of soil microorganisms may apply not only to their effects on soil but also on vegetation.

Jenny (1941: 199–200) concluded that the soil microflora may be considered a constant independent factor in soil formation because it is potentially about the same throughout the world. That is, in the course of many decades all soils are repeatedly inoculated by all kinds of microorganisms. Potential microfloras, o_m , seemingly are identical. This rather startling postulate of Jenny's has been supported by Feher and Frank (1947): "The most common species of soil bacteria appear to be worldwide in their distribution, the same species occurring in the different soil types and geographical areas of the world. They are probably absolutely ubiquitous." It does not follow that all soils have identical microbial populations. On the contrary, the number of each microbial species living in soils varies from soil to soil, because growth is a dependent variable. Too, parasite numbers differ between soils—but parasites by definition are dependent. Also dependent are the relations between groups of microorganisms in the soil. Differences between soils and vegetations on two different sites cannot be caused by the variations in microorganism populations found in the soils of the two sites because the microorganism differences depend—as do the soil and vegetation differences—on the environmental factors operative on the two sites.

Tentatively we can adhere to Jenny's postulate that the independent aspect

of the microorganism factor, o_m , is the same for all soils and all vegetations.

The factor time

Vegetation changes with time. In any natural plant cover time changes may occur at 5 definable levels (Iaroshenko 1946): 1) seasonal, evidenced as aspeption; 2) annual, related to the variations of meteorological and biotic factors; 3) successional, or the time series of plant communities on some specific locality; 4) historical, or the alternation of types of plant communities in some specific region during a series of geological epochs; 5) genetics of plant communities, or the evolution of various phytocoenoses from an earlier vegetation. Diurnal changes in the plant cover may be added, but these influence neither vegetation nor flora as commonly considered.

The last two of Iaroshenko's items are historical changes in the flora, on a geological time scale. They seem to involve times of an order of magnitude at least greater than 1,000 years. On the other hand, succession as defined above seems to stabilize most vegetation within periods of less than 1,000 years. Thus, succession and the "historical" factors are definably different, and the amounts of time necessary for each process differ by a factor whose lower limit approximates 10. The first two aspects of time changes show periods with orders of magnitude of one and less than 20 years, respectively. This paper is not concerned with these rapid fluctuations in vegetation due to seasonal or annual variations. It is concerned with plant succession, for this is an effect of time evidenced by changes which are contemporaneously observable yet are not so rapid as to be classed as oscillations. Also, plant succession seems to go in a definite and determinable direction in a given ecosystem and produces a plateau of little change, stabilized vegetation. Definite and determinable direction, relative end stage, etc., are not

characteristics of the other time changes in the earth's plant cover named by Iaroshenko.

In other words, there are various kinds of change in vegetation with time. If all such changes are called "succession," important differences are obscured. Succession is defined here as a particular kind of change in vegetation with time. It is a progressive process with a marked time zero.² The historical changes in vegetation have no such well-marked time zero unless caused by introduction of a single, dominant new organism, such as the chestnut-blight, into the ecosystem.

Professor Herbert L. Mason in lectures on changes in the plant cover refers to its ontogeny those changes we here name succession and to its phylogeny those changes we here name historical. The splitting of time changes in the plant cover into two levels was recognized by Braun-Blanquet (1932: 336) who named the historical aspect "secular succession," and the other "present-day" (called "actual succession" by Lüdi 1932: 535, "recent succession" by Etter 1947). Sukachev (1944) uses the terms "syngensis" and "cenogenesis" for recent and secular succession, respectively.

Finally, succession as here defined produces changes directly in *vegetation*; the historical factors produce changes directly in the *flora* and only secondarily in vegetation. We have found it necessary to use the flora as one of the environmental factors determining vegetation. Only *through* changes in the

² Time zero in primary succession may be taken as the first occurrence of plant disseminules in the bare area; for secondary succession as the first occurrence of plant disseminules in the area bared, wholly or partially, by whatever catastrophe destroyed or markedly changed the vegetation. The same time zero probably should be used for studies of soil changes with time. In general, a new time zero must be chosen whenever one of the environmental factors changes suddenly and with great effect on the vegetation or soil.

independent determining factors—the flora, climate, soil parent material, relief, or human activity—do the historical factors affect vegetation. Successional change as here defined is a time change unique to vegetation, *i.e.*, to plant communities. This certainly doesn't preclude use, including definition, of the term by zoologists.

The definition of succession used here is not intended to minimize the effects of historical changes in climate on vegetation. But such effects can only be evaluated after we know the effects on vegetation of regional differences in climate.

"Soil or edaphic factor"

It will be noted that, contrary to expectation, the factor soil is not contained in equations (2) and (3) although obviously soil and vegetation always mutually influence each other. Strictly speaking, in nature one cannot separate the effects of one from the effects of the other since the same set of conditioning factors pertains to both soil and vegetation. Both soil and vegetation vary with time and both are determined by *cl*, *p*, *r*, and *o*. Both vegetation and soil are dependent variables. They depend

for their nature on the very same thing, the nature of the ecosystem or landscape.

Dokuchaiev and Hilgard, pioneers of Russian and American soil science, stated the dependence of soil on the landscape factors. Schimper similarly was a pioneer plant ecologist and pointed out the dependence of vegetation on factors of the environment. We can conclude the landscape or ecosystem is a plexus of a set of environmental factors which determine *both* vegetation and soil. Data so far show that on a given rock in a given landscape with a common flora a particular vegetation develops, so does a particular soil. Table I gives an example. This example illustrates a case of parallel development of soil and vegetation in a particular ecosystem. Causation between soil and vegetation is not implied.

Ecologists may profit by working with the concept of parent material rather than soil, for only the parent material of a soil is independent of the other landscape or ecosystem properties which determine both vegetation and soil. Soil properties such as acidity, organic matter content, depth, etc., are not independent factors but are determined by the same set of landscape factors which determine such properties of

TABLE I. *Parallelism between plant succession and soil development in the limestone Alps of the Engadine, Switzerland. After Braun-Blanquet and Jenny (Jenny 1941: 218)*

Development of vegetation			Development of soil				
Stage	Plant association	Relative production of organic matter, per cent	pH	Total acidity, milli-equivalents per 100 g.	Organic matter of surface soil, per cent	Thickness of humus layer, centimeters	General description of soils
Initial	Firmetum	40	7.2 ± 0.04	0	0-30	0-5	Disintegrated and slightly weathered limestone rock
Transitional	Elynetum, Festucetum	100	6.1 ± 1.07	1.3	20-50	10-30	Rendzina* profile, leaching of lime, humus accumulation
Climax	Curvuletum	60	4.8 ± 0.03	7.2	20-60	10-100	Alpine humus soil, leached profile, acid humus

* Since 1944 the Zürich pedologists headed by Pallmann have differentiated rendzina soils (developed from soft, clay-rich limestones) from Humuskarbonat soils (developed from hard limestones, poor in silica and clay). Cf. Leuenberger (1950).

vegetation as species list, weight production, cover, physiognomy, etc.

"Competition factor"

Competition is obviously a factor in determining where and when a particular plant or plant community occurs (Braun-Blanquet 1932: 82). But it is not an independent factor. Plant competition occurs only in the presence of vegetation—a tautology of course. A floristic list for the vegetation, defining ϕ , is a measure of the competition factor. It expresses potential intra- and interspecific competition. Since competition cannot be construed as a factor determining vegetation independent of the five ecosystem factors, it is not to be found in equations (2) and (3).

VEGETATION FUNCTIONS AND SEQUENCES

By holding³ all environmental factors but one the same throughout a series of ecosystems, variations in vegetation caused by that one factor may be studied. Five possible types of functions, using v values, can be obtained. Also, five types of sequences, using V values, occur (Jenny 1946). These functions and sequences are listed and named in Table II. Climofunctions can obviously be split into hydro- and thermofunctions; similarly biofunctions can be divided into floro-, zoo-, and homofunctions with corresponding se-

quences. Further subdivision of these principal functions can well wait on at least preliminary solution of those named or demonstration that these are inadequate. Functions involving microorganisms are purposely omitted altogether for reasons already stated. In each of the tabulated cases the chosen variable factor is enclosed in parentheses; the remaining four ecosystem factors which are the same throughout the function or sequence are written as subscripts.

The functions are to be understood as having the ordinary properties of most mathematical functions—continuity, differentiability, possibility of graphic portrayal, quantitative statement, etc. Usual mathematical methods may be applied both to individual functions and the general fundamental equation (2). The sequences on the other hand are qualitative series.

A mathematical approach is used in this paper because it offers a method of abstracting concepts from their verbal definitions, a universal notation, a logical system of manipulating concepts, and the ultimate opportunity to replace qualitative by quantitative data.

In each function or sequence, 4 of the 5 environmental factors are postulated to be the same throughout. But the ecologist is extremely fortunate who finds a series of landscapes where only one of the environmental factors varies⁴ and all others do not. However, absolute constancy of all factors but one need not be insisted on in order to study the effects of that one factor on vegetation. A property of vegetation or a plant community can be approximated as a function of only one independent factor, in Jenny's (1946) words, as the "result of the following two possibilities: 1) the one factor varies greatly while the

³ No experimental approach is implied. Plant ecology is primarily a field study and to allow only one environmental factor to vary, areas (ecosystems or landscapes) must be chosen where this occurs naturally. Such methodology is discussed by Jenny (1930, 1941, 1946). In other words, in any one function or sequence, four of the five groups of environmental factors do not effectively vary; in a mathematical sense they are "constant" even though they are factors with a pronounced annual, or even diurnal, periodicity such as temperature; they are the same throughout the sequence. If the forms of functions which express effects of the environmental factors were known, statistical methods of eliminating variables could be used.

⁴ "Varies" in the sense that it has different values in the various landscapes. The factor may have a periodical march in any one landscape.

TABLE II. Possible kinds of vegetation functions and sequences

Functions (quantitative mathematical relationships)		Sequences (qualitative series)	
$v = f(cl)_{p, r, o, t}$	Climofunction	$V = f(cl)_{p, r, o, t}$	Climosequence
$v = f(p)_{cl, r, o, t}$	Lithofunction	$V = f(p)_{cl, r, o, t}$	Lithosequence
$v = f(r)_{cl, p, o, t}$	Topofunction	$V = f(r)_{cl, p, o, t}$	Toposequence
$v = f(o)_{cl, p, r, t}$	Biofunction	$V = f(o)_{cl, p, r, t}$	Biosequence
$v = f(t)_{cl, p, r, o}$	Chronofunction	$V = f(t)_{cl, p, r, o}$	Chronosequence

remaining ones vary, in comparison, but little. 2) save for the one function, the slopes of the others are nearly zero. In other words, some factors may vary considerably, yet be of relatively little importance in determining differences in soil [or vegetation] properties."

The reasoning behind Jenny's statement can be understood by totally differentiating our fundamental equation (2) giving:

$$dv = (\partial v / \partial cl) dcl + (\partial v / \partial p) dp + (\partial v / \partial r) dr + (\partial v / \partial o) do + (\partial v / \partial t) dt. \quad (4)$$

That is, to determine a change in a property of vegetation (dv) we must determine the changes in the five independent variables, the differentials dcl , dp , dr , etc., in practice often replaced by Δcl , Δp , Δr , etc., and in addition also determine the five rates of change of the vegetal property with the independent variables, the partial coefficients $\partial v / \partial cl$, $\partial v / \partial p$, $\partial v / \partial r$, etc. A complete statement of a vegetal property function is:

$$v_2 - v_1 = \int_a^b (\partial v / \partial cl) dcl + \int_c^d (\partial v / \partial p) dp + \int_e^f (\partial v / \partial r) dr + \int_g^h (\partial v / \partial o) do + \int_i^j (\partial v / \partial t) dt. \quad (5)$$

It would be very difficult to solve this equation completely, but we can hope to approximate it or solve certain parts.

The differential equation (4) permits a complete statement of the problem of isolating the variables. To set up a change in vegetation, v , as a function of say, climate only, just v and cl can appear in the differential equation, *i.e.*, we must

be able to write:

$$dv = \frac{\partial v}{\partial cl} dcl \text{ or } v = F(cl)_{p, r, o, t}.$$

Evidently the four products $(\partial v / \partial p) dp$, $(\partial v / \partial r) dr$, $(\partial v / \partial o) do$, and $(\partial v / \partial t) dt$ must equal zero. This can be accomplished in either of two ways. First, dp , dr , do , and dt can all equal zero. This means these variables p , r , o , and t do not change. Or, $\partial v / \partial p$, $\partial v / \partial r$, $\partial v / \partial o$, and $\partial v / \partial t$ can all equal zero. This means that the rates of change of the property of vegetation with respect to these four independent variables are zero. Obviously any combination of the differentials equaling zero and the partial coefficients also equaling zero is possible, just so the respective products of partial coefficient and differentials all equal zero.

In words, the partials are simply the effects of the independent on the dependent variable; $\partial v / \partial cl$ is the effect of climate on vegetation. Rigorously, however, $\partial v / \partial cl$ is the rate of change of a property of vegetation, represented by v , with respect to a climatic measure, represented by cl , holding the factors climate in all its other aspects, soil parent material, relief, biota, and time in all their aspects constant. "The partial of v with respect to cl " is shorter and simpler; " $\partial v / \partial cl$ " is still better. Both of the latter are rigorous.

This differential nomenclature may appear forbidding. However, it is precise, logical, neat, space-saving, and lends itself readily to mathematical and logical manipulation. It appears useful.

Plant ecology is not concerned merely with investigating the effect of one factor on vegetation. It often wants to analyze why an observed difference between the vegetation on two sites

exists. We can use equation (5) as the basis for discussion. The difference $v_2 - v_1$ has been observed. The problem is why does this difference exist? Obviously the factors of the environment must be known. Cl , p , r , o , and t represent only groups of factors. Much analysis and definition must be done within these groups before a complete list of habitat factors for any given ecosystem can be drawn up. Given the habitat factors, do they differ between the investigated sites? In other words, do the differentials exist? Now, within what limits do the environmental factors exist; what are the limits of integration for each variable? Finally, what is the influence of each variable on the vegetation characteristic being investigated; what values have the partials? Information of the above three kinds for each determining factor is necessary for the solution of the problem presented by differences in vegetation on different sites.

Below are given a few examples of functions and sequences. Many others are of course known. Following each description of a sequence, such as the climosequence $V = f(Cl)_p, r, o, t$ is a short description of the factors which do not effectively vary in the sequence being discussed. In a climosequence the levels of p , r , o , and t would be stated.

Illustrations of climosequences

As pointed out in the discussion of climate, the variables moisture and temperature can influence vegetation independently.

The Great Plains area contains excellent examples of moisture sequences. Along an isotherm, say 11°C (52°F) annual temperature, the vegetation changes with increasing precipitation from shortgrass, to midgrasses, to tall bunchgrasses, and finally in the easternmost and wettest part to tall bluestem sod. This sequence is illustrated by Jenny (1941: 210, Fig. 104). The moisture boundaries of these communi-

ties are approximately 17 inches precipitation a year for shortgrass, 17–21 inches for the midgrasses, 21–27 inches for tall bunchgrass, and 27–38 inches for bluestem sod. Most ecologists would probably say that these changes in vegetation are related to the precipitation differences. Then the influence of the other environmental factors must be nil or these factors must not vary. The former alternative seems more improbable than the latter. Therefore we find some justification for saying that the factors other than precipitation are relatively constant throughout the sequence: $T = 11^\circ \text{C}$ as mentioned, p = loess and other windblown materials, r = undulating, o_f = one Great Plains flora for the whole area, o_s = no overgrazing, t = the same for all the grassland types and approximating a few thousand years since the latest major climatic change, the postglacial xerothermic period.

In the same region Weaver's (1924) data on three years' (1920–1922) average annual production of virgin grasslands show a striking increase in yield with increasing moisture (Fig. 1). The other environmental factors are the same throughout, or their differences are too small to be effective, evidently. They are listed below:

T (Temperature) = $10\text{--}12^\circ \text{C}$ mean annual; potential evapo-transpiration, calculated by Thornthwaite's method (1948), is 68.5 cm of water per year for Burlington, 77.5 Phillipsburg, and 74.0 Lincoln

p , r , and o as above

t = unknown but of no influence. Plant communities corresponding to Weaver's three have been described as climax in these areas. The climax is stable; it is the stable stage of a sere. Thus there are no successional changes in climax vegetation. The effect of time, according to our definition, is nil in the climax; $\frac{\partial v}{\partial t}$ in the climax approaches zero.

For the stations listed in Figure 1, temperature is not exactly the same throughout. However, yields of prairie hay are not significantly correlated with

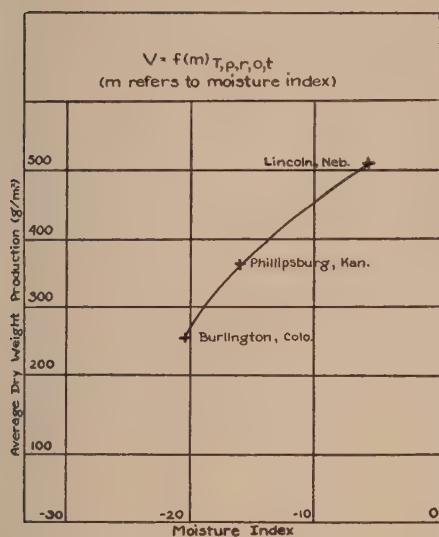


FIG. 1. Average dry weight production of virgin grasslands in the Great Plains correlated with moisture, other environmental factors not effectively varying. Production data from Weaver (1924), included approximately 50 meter square quadrats per year per site. Moisture indices calculated by Thornthwaite's method (1948). Mean annual precipitations are Burlington 420 mm, Phillipsburg 570 mm, and Lincoln 690 mm. A curve of constantly decreasing slope is more reasonable than a straight line; i.e., $dv/dm = k/m$ or $v = a + b \ln m$.

mean annual temperatures (Jenny 1941: 213, Fig. 105); the partial derivative $\partial v/\partial T$ therefore approximates zero. In other words, the temperature variation from 10 to 12° C which occurs among Weaver's three stations probably does not materially influence vegetation weights and can therefore be neglected.

Moisture sequences caused by rain shadow effects can be readily found. Vegetation and moisture across the north-south extending Pahvant Plateau of Central Utah are diagrammed in Figure 2. The two plant communities, sagebrush and shadscale, are determined by differences in moisture (Billings 1949). They exhibit a true moisture sequence because the determining factors other than precipitation are nearly the same at both places:

$T = 9.2^\circ \text{ C}$ (Richfield) to 11.0° C . (Fillmore) mean annual; 62.8 cm of water per year (R.) to 69.7 (F.) potential evapo-transpiration.

This difference we assume to be negligible

p = alluvium from red sandstones and shales
 r = gently sloping alluvial fans

o_f = a Great Basin flora. No floristic barriers, to the dominants at least, exist

o_z = grazed moderately

o_h = not burned, plowed, overgrazed, etc.; substantially natural conditions

t = long enough so $\partial V/\partial t$ is negligible.

A temperature sequence is shown by the plant communities at St. George and Frisco in southwestern Utah. The *Larrea tridentata* community at St. George contrasts with the *Artemisia nova-Atriplex confertifolia* community to the north at Frisco. In St. George potential evapo-transpiration (Thornthwaite's measure of temperature effectiveness, 1948) is 87.7 cm of water per year, in Frisco 66.5 cm. Mean annual temperatures are 15.2° C (St. G.), and 10.0° C (F.).

The black sagebrush-shadscale community is the characteristic representative of the northern desert shrub zone which is in all respects save temperature regime comparable with the creosote bush community farther south. Other communities of the northern desert shrub zone are unduly influenced by saline ground water and soil (pure shadscale, greasewood), by overgrazing (little rabbitbrush), or by the wetter climate

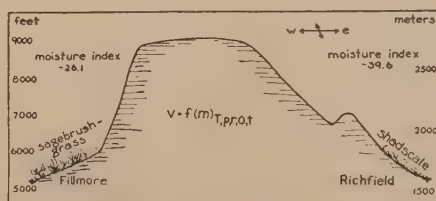


FIG. 2. An east-west transect across the Pahvant Plateau in central Utah showing a moisture sequence of plant communities. Seasonal distribution of precipitation is the same at both Fillmore and Richfield; mean annual precipitations are: F. = 367 mm and R. = 212 mm (U. S. Weather Bureau). Moisture indices were calculated by Thornthwaite's method (1948).

or rockier soil of benchlands (pinyon-juniper), and are therefore not suitable for comparison.

The factors other than temperature are the same at St. George and Frisco or their differences are too small to be effective:

m (moisture) = 208 mm (F.), and 218 mm (St. G.) mean annual precipitation, with very similar distributions. Thornthwaite's moisture index ranges only from -41.2 (F.) to -45.0 (St. G.)

p = alluvium from tertiary extrusives of chemically intermediate or mineralogically mixed composition (Butler *et al.* 1920)

r = alluvial fans, bajadas; the playas and lower mountain slopes have different vegetation

o_f = a southern Great Basin flora; the Pine Valley mountains north of St. George have probably not been a barrier to the dominants

o_s = protected from overgrazing

t = long enough so stable vegetation has developed; $\partial V/\partial t$ is negligible.

Illustrations of lithosequences

In these sequences vegetation is related to soil parent material; cl , r , o , and t must remain constant or if they do differ, then ineffectively.

Tüxen and Diemont (1937) describe a "Klimaxgruppe" of plant communities from northwestern Germany. These are lithosequences of stable communities which differ because of variations in soil parent materials. On Cretaceous limestone occurs the Querceto-Carpinetum primuletosum, on calcareous loess the Querceto sessiliflorae-Betuletum typicum. Tüxen and Diemont say (p. 81), "Similar examples of a strong mosaic of terminal communities on level surfaces with old soils and within the same climatic region, which are conditioned only by alternations of soil parent material, are to be found everywhere in northwest Germany, what is more, also in northwest and central Europe. Neither soil formation nor development of vegetation in our region can by their effects on [micro-] climates fully equalize the effects of the petrographic properties of the 3 principal groups of soil parent material rocks: limestone, silicate rocks,

and quartz sand." In this example, of the five factors cl , p , r , o , and t , only p varies effectively.

Illustrations of toposequences

Toposequences due to slope exposure differences are clearly evident in arid mountains. Shreve's (1915) example is classic. In the Santa Catalina Mountains of southern Arizona at several topographic levels vegetation is strikingly different on north and south slopes of ridges. The situation is diagrammed in Figure 3. At 8,000 ft altitude yellow pine forest on the south exposures contrasts with fir on the north, at 6,100 ft evergreen oaks with yellow pine, at 4,200 ft desert vegetation with evergreen oaks.

The pertinent area of the mountain can be described as follows:

cl = the same within each topographic level, such as 8,000, 6,100, and 4,200 ft

p = gneiss throughout

r = the same except for the single topographic factor, exposure; at least Shreve makes no differentiation of vegetation in relation to degree, length, or shape of slopes

o = probably one flora throughout; certainly in each altitudinal (climatic) zone within which the vegetation contrasts on north and south slopes, the flora is the same clear around the mountain; the north slope flora does not differ from the south slope flora, only vegetations differ

t = such that essentially stability has been attained throughout, at least in the dominants; $\partial V/\partial t$ approaching zero and therefore negligible.

At other elevations there may be no differences between the vegetation of

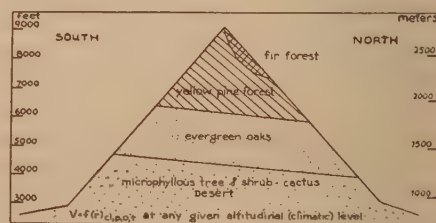


FIG. 3. Differences in vegetation on contrasted exposures in the Santa Catalina Mountains of southern Arizona (from Shreve 1915: 12).

north and south slopes. Thus, below 3,900 ft is desert, at 4,700 to 5,800 ft is evergreen oak, at 6,300 to 7,300 ft is yellow pine forest on both north and south exposures. At elevations within these altitudinal limits regional (average of the altitudinal) climate determines type of vegetation; in the exposure ecotones local climate is decisive and is a function of slope exposure.

Tüxen and Diemont (1937) designate as "Klimaxschwarm" the group of stable communities differentiated by slope exposure from the *Fagetum boreoatlanticum* in the Harz mountains. "Mapping of vegetation has shown that the distribution of these communities (and their soil profiles) is regularly related to the different slope exposures so that the *Fagetum dryopteridetosum* occurs on north and northeast slopes, the *Fagetum festucetosum* in general on summits and gently sloping northwest to north slopes, the *Fagetum luzuletosum* on northwest and southeast slopes (*Calamagrostis-Poa Chaixii* Fazies) and on the gently sloping west and southwest slopes (*Luzula-Deschampsia* Fazies), and finally the *Querceto-Betuletum* on the steep south to southwest slopes." This toposequence is diagrammed in Figure 4. Throughout the sequence *cl*, *p*, *t*, and *o* do not vary effectively.

Depth and duration of the winter snow cover have been used in Swedish Lapland to explain distributions of vegetation (Du Rietz 1950). Deep snow insulates ground vegetation against extreme cold and drying; a long-continued snow cover shortens the growing season.

In the lower Alpine zone, a *Vaccinium myrtillus* community is found in sheltered spots where snow is not removed by the wind; a *Loiseleuria-Diapensia* community occupies exposed spots where the snow is blown away by the wind; a *Salicetum herbaceae* occurs where the growing season is drastically shortened by heavy snow accumulation. Areas including these three plant communities

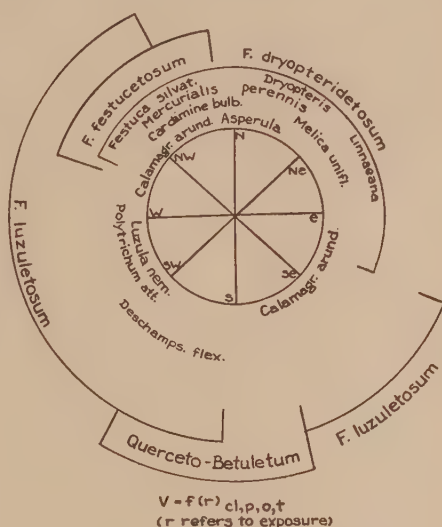


FIG. 4. Dependence of the subassociations and facies of the *Fagetum boreoatlanticum* in the Harz mountains on various directions of slope exposure (from Tüxen and Diemont 1937).

may be selected in such a manner that *cl*, *p*, *o*, and *t* do not vary effectively. Variations in wind, associated with relief, are responsible for the differences in snow accumulation within this climatically fairly uniform region. Snow accumulation is thus a function of relief. Therefore, these three communities form a toposequence.

Illustrations of biosequences

Some sequences of plant communities are associated with differences in floras. That is, a florosequence is due to a significant difference in the floristic factor.

A flora is composed of individual species, each with its individual distribution. Species distributions may show gaps or discontinuities due not only to the phylogenetic and geological history of the species but also to physical barriers to migration or to lags in that migration caused by past climatic changes, such as a glacial or xerothermic period. As already noted, migration of species is generally an historical process on a

geological, not successional, time scale. Succession is treated in the next section under chronosequences. The results of plant migrations are areas with different floras, producing florosequences. In accord with the definition of the floristic factor given previously, local discontinuities in the environmental factors which may determine a species' local existence do not directly determine the limits of a flora, for existence is a dependent feature of vegetation; disseminule distribution is independent of such environmental discontinuities over contiguous areas.

Differences in vegetation due to the differences in floras caused by migration or isolation have been qualitatively described. Ramaley (1931) ascribed the present northern limit of *Quercus gambelii* in the foothills east of Denver, Colorado, to historical, not climatic factors. The alpine and subalpine vegetation of the Uinta mountains in Utah differs from that of the adjacent Wasatch mountains by having in its flora some 72 species not found in the latter range, including such prominent alpine and subalpine species as *Elyna* (*Kobresia*) *bellardi*, *Trollius albiflorus*, *Papaver radiculatum*, *Sedum rhodanthum*, *Kalmia microphylla*, etc. The floristic differentiation probably results from Pleistocene glaciation with its attendant plant migrations and exterminations. Although the Uinta mountains are more massive, higher, and less dissected than the Wasatch mountains, alpine and subalpine landscapes which are similar with respect to the factors cl , p , r , o_h , and t can be found in both ranges. Since the alpine floras of these ranges differ, their alpine plant communities are distinctive and are members of a florosequence.

The essential problem in establishing florosequences is to correlate differences in species ranges with differences in vegetation communities, the factors cl , p , r , and t being constant or ineffectively varying.

Homosequences are common. Samp-

son (1919) described several "weed stages" in the subalpine zone of the Wasatch Plateau of central Utah. These stages resulted from various degrees of overgrazing by domestic stock, mostly sheep. They are steps in an intensity-of-grazing sequence. Ellison (1947) has pointed out that on the Wasatch Plateau today a vegetation sequence occurs which is related to the class of stock grazed—sheep producing a narrow-leaved grassland, cattle a plant community of broadleaved forbs.

In these grazing sequences, if the plant communities were not stable, natural plant succession would play a role in determining them. This would involve the factor time. But the plant communities named are stable under the given levels of o_h . Thus, Sampson's "weed stages" and Ellison's grass *vs.* forb communities are the result of predominance of the factor o_h above all other environmental factors. The influence of grazing herds is continuous, and the partial $\partial V/\partial o_h$ overshadows the partial $\partial V/\partial t$ (natural plant succession). The natural plant successions have not been worked out thoroughly enough in a quantitative way to separate precisely the changes in vegetation into what is natural and what man-caused.

Many other sequences of vegetation due to man's activity are well known. These include secondary seres in forests, grasslands, arable land, etc. In such seres separation of the partials $\partial V/\partial t$ (natural plant succession) and $\partial V/\partial o_h$ (civilized man's continuing influence) is certainly not easy, but it appears to be a necessary step in planned land management.

Illustrations of chronosequences

By means of dated photographs Ives (1941) traced the development of a burned spruce-fir forest in Colorado to brush, through an aspen stand, and back to spruce-fir. In this well-dated case the single landscape studied has had one essentially constant set of cl , p , r , and o

throughout the sequence, which is therefore an excellent chronosequence, however qualitative in its description of the vegetation concerned.

Unfortunately succession has not always been studied by making consecutive observations on one area. Instead inferential methods have been used. The present reaction against the use of deductive reasoning in plant ecology (Cain 1947) seems to be a reaction in part against exclusively inferential methods of investigating succession.

Besides this methodological problem there exists another difficulty in studying succession, the collecting of quantitative data on vegetation. Without quantitative data, it is impossible to establish chronofunctions. Without chronofunctions, as contrasted to chronosequences, predictions cannot be precise and details of the process of succession remain obscure. To be specific, what is the shape of succession-time curves? Cooper (1926: 403) almost 25 years ago said that succession "in rate, too, is more or less subject to rule, an initial increase, a medial maximum, and a long decrease in rapidity of change being characteristic." Most ecologists would probably concur. Data to illustrate the rule, however, are few. Moreover, it is not always clear what property of vegetation can be measured and plotted against time to yield a curve. The question of curve shape is not merely academic since if we know what type of equation describes a curve, very few points are necessary to approximate the constants of the curve. Given the curve's constants, predictions can be made—later to be checked against field data. Thus, theories and generalizations can be tested.

Of those successional data which meet both the above objectives of consecutive observations on one area and quantitative nature, some of Cooper's (1939) from permanent quadrats on the shores of Glacier Bay, Alaska, are graphed in Figure 5. In these chronofunctions v is the number of stems per unit area.

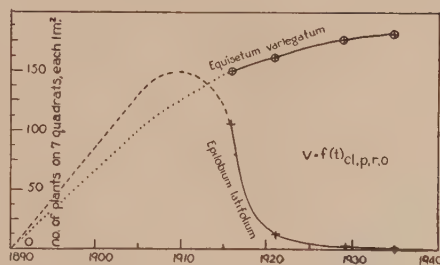


FIG. 5. Numbers of plants on seven 1 m² quadrats at Glacier Bay, Alaska, as a function of time (from Cooper 1939). Time zero is 1879 for two plots, 1892 for two plots and 1899 for three plots, with the average, 1891 (dates kindly supplied by Dr. D. B. Lawrence). The dotted lines are purely hypothetical.

Evidently *Equisetum variegatum* has been increasing in abundance. However, its rate of increase is decreasing. That is, the partial $\partial v / \partial t$ (slope) although positive is slowly approaching zero. Thus, the number of shoots of *Equisetum* may be approaching a maximum. On the other hand, the number of *Epilobium latifolium* shoots is decreasing to zero. The partial $\partial v / \partial t$ is negative and decreasing in absolute amount. Presumably *Epilobium* has passed a maximum. But there is a considerable gap in the data between time zero (deglaciation) and the first records. The quadrats were laid out in vegetation already in a pioneer stage. Thus, it is unsafe to speculate very much on the basis of the few available observations. The dotted lines are purely hypothetical.

Of course any seral species would show a maximum in its curve of abundance against time; the curve should have a hump. A seral species first increases, then decreases in abundance. As it increases the slope, $\partial v / \partial t$, is positive; at the maximum $\partial v / \partial t$ is zero; as it decreases $\partial v / \partial t$ is negative; and finally as v approaches zero so may $\partial v / \partial t$ also. Species of stable vegetation, however, should show only one branch of this humped curve. They increase, probably asymptotically, to their mean stable abundance. For such species $\partial v / \partial t$ re-

mains positive, but approaches zero. The data quoted have all covered too short a period of time to exhibit the complete hypothesized curve for any species. *Equisetum* at Glacier Bay may be on the ascending branch, *Epilobium* on the descending. The hypothetical curves were drawn on this basis.

The two cases cited above are concerned with primary succession. Secondary succession is being recorded by permanent quadrats in the subalpine zone of the Wasatch Plateau in Utah by the U. S. Forest Service. This secondary succession was induced at the turn of the century as a result of destruction of the plant cover by grazing and subsequent protection. Data from these quadrats extend over a 30 year period and show humped curves for certain species. *Achillea lanulosa*, notably a seral species and almost the only perennial one on these quadrats when they were established around 1916, shows this hump. Interestingly enough, it appears that *Agropyron trachycaulum* does also. Early in the period of study of this area Sampson (1919) concluded that *Agropyron* was climax. His argument was based largely on the comparative physiology, as judged from their growth forms, of the dominant species. Ellison (1947), on the basis of the quadrat record available after 20 additional years and by analogy with long-protected natural areas that he found, believed *Agropyron* was not climax over much of the area. The criterion mentioned above of deciding when a species is seral and when a member of stable vegetation supports Ellison's thesis.

The Wasatch Plateau records are complicated by yearly climatic irregularities and, as Ellison (1943) has said, by continued accelerated soil erosion. However, accelerated soil erosion is probably not an independent factor in mountain secondary plant succession. Abundant data show that a well-developed vegetative cover lessens runoff

and soil erosion on slopes. Therefore, any denuded site on a slope will be eroded at an accelerated rate. And so no change in such secondary vegetation can be assigned to soil erosion as such. Erosion is not an independent factor. As already pointed out, in a given ecosystem changes of vegetation and soil cannot be separated.

Many quantitative successional data employ a relative time scale, only. This is notably true of the work of Braun-Blanquet and Jenny in the Swiss National Park (*cf.* table I) where pH of the soil is a function of relative time. The quantitative functional relationship, $\text{pH} = f(\text{time})$, could not be evaluated.

PARALLELISM OF SOIL FORMATION AND PLANT SUCCESSION

Both soil and vegetation are functions of five groups of factors. A vegetation and a soil property can be correlated only in the special case where four of the five groups of determining factors are constant in effects. Thus, in general no soil property can be universally correlated with a property of vegetation (Jenny 1941: 267-9). In general vegetation is not a function of soil; soil is not a function of vegetation. Both the soil and vegetation of a particular landscape are functions of the factors of that landscape, that site, that ecosystem, that environment—whichever term is preferred. Soil will be a function of σ_f , the flora which is an independent ecosystem factor, when cl , p , r , t , and the other aspects of σ are constant or ineffectively varying. But then vegetation will also be a function of σ_f .

While a soil may exist without vegetation as a special case, judging from current definitions soil formation seems to be impossible without vegetation. Jenny (1941: 17) defines soil in terms of his fundamental equation (1) in which the flora explicitly enters. Presence of a flora means vegetation is also present (v at t_0 is disseminules). Some Russian

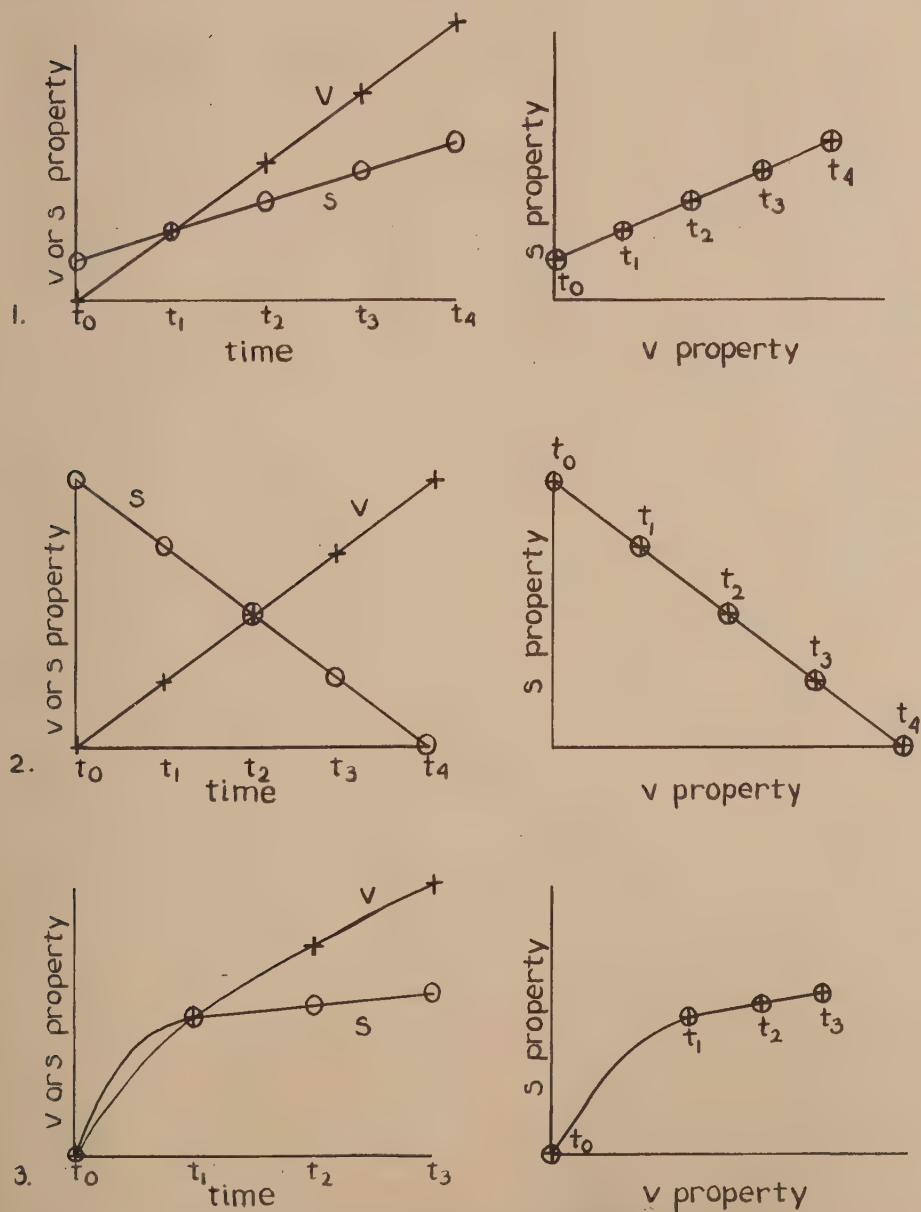


FIG. 6. Illustrating for a given ecosystem with cl , p , r , and o constant. 1—Soil formation and vegetation succession both progressing with time in the same direction, differing only in rate, standard error of estimate of the equation $s = \varphi(v)$ is zero. 2—Soil formation and vegetation succession progressing with time with slopes equal but one positive (v) and the other negative (s); standard error of estimate of the equation $s = \varphi(v)$ is still zero. 3—Curvilinear development of soil and vegetation with time (the probable case); standard error of estimate of the equation $s = \varphi(v)$ is zero (v can represent weight of vegetation per unit area; s can be percentage nitrogen in the surface 20 cm of the soil).

pedologists (Vilensky 1937) simply define soil as the result of the interaction of mother rock and the biosphere. Pallmann (1948: 60) defines soil as "the polydisperse, loose layer of the solid earth's crust that arises through physical and chemical weathering of rock, humus formation, and various translocations of the products of weathering and humus formation." Humus comes only from vegetation. Finally, zero time of soil formation may also be considered zero time of plant succession. Under the definitions of soil quoted, the reverse is also true.

Thus we may conclude that in a given landscape, soil formation cannot be separated from vegetative succession. Both processes are related to the time sequence of events determined by the particular levels of cl , p , r , and o obtaining in the particular ecosystem. In a given ecosystem characterized by specific values of cl , p , r , and o , say cl_x , p_y , r_z , o_n , soil and vegetation develop simultaneously. A given soil property, s , changes with time, symbolized as:

$$s = f_s(t)_{cl_x, p_y, r_z, o_n} \quad (6)$$

A given property of vegetation, v , also changes with time in accordance with the formal equation:

$$v = f_v(t)_{cl_x, p_y, r_z, o_n} \quad (7)$$

The left hand curves of Figure 6 illustrate equations (6) and (7), *i.e.*, some possible functional relationships of soil formation and vegetation succession with time.

The right-hand curves of Figure 6 are plots of the equations obtained by eliminating t from equations (6) and (7) giving $s = \varphi(v)$, or $v = \psi(s)$. Note that in Figure 6, part 2 could be made to show not only perfect correlation between soil and vegetation development but also absolute coincidence in these developments by reversing the scale used to measure s .

In other words, in a specific ecosystem or landscape, soil and vegetation develop

together and in the same direction. The nature of their functional relations with time determines how nearly parallel they develop. Such parallelism between soil formation and plant succession was found by Braun-Blanquet and Jenny (*cf.* table I) in the alpine zone of the Alps and by Braun-Blanquet in the Mediterranean region (1933). Braun-Blanquet (*cf.* also his colleague Tüxen 1931/32: 183) made the generalization of parallel development of soil and vegetation on empirical grounds; theory agrees.

SUMMARY

Starting from the definition of plant ecology which says that vegetation is conditioned by five groups of factors, here taken to be climate, soil, topography, biota, and time, substitution of Jenny's soil forming factor equation and appropriate definition lead to a systematization of plant ecology expressible by the equation: V or $v = f(cl, p, r, o, t)$. V represents a plant community, v a property of vegetation; f is "a function of"; cl is regional climate; p is soil parent material; r is relief or topography; o is the biota; t is time.

Use of this fundamental equation makes possible closer and more accurate delimitation of the factors determining vegetation, provides a frame within which quantitative data on vegetation can be collected, offers methods of manipulating such quantitative data, and finally also offers methods of manipulating the symbols representing ecological abstractions.

Vegetation is dependent on the five mathematically independent groups of factors represented by cl , p , r , o , and t . These factors determine a particular kind of system, an ecosystem or natural landscape.

For the purposes of this paper the following definitions are used:

cl is regional climate; local or topographic climate is a function of relief; microclimate or

phytoclimate is a dependent property of vegetation

p is the state of the soil system at time zero

r has reference to degree, solar direction, length, and shape of slope, independent aspects of ground water and snow cover depth and duration

o can be subdivided into o_f , representing the flora or the summation of plant disseminules reaching the site; o_z or fauna, including o_h or the influences of man; and o_m or the effectively constant influence of microorganisms.

Sequences of plant communities or vegetal property functions can be recognized and named according to one factor which changes while the others do not change effectively. Thus, changes in vegetation can be ascribed to one cause.

From mathematically considering the equations: $s = f_s(cl, p, r, o, t)$, and $v = f_v(cl, p, r, o, t)$, we may conclude there are no universal correlations between vegetation and soil; in such a system soil is not determined by vegetation, vegetation is not determined by soil; vegetation and soil develop concomitantly.

LITERATURE CITED

- Bailey, R. W. 1939. Mountain floods and vegetation. Proc. of 6th Pacific Sci. Cong. 4: 731-736.
- Billings, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. Amer. Midl. Nat. 42: 87-109.
- Braun-Blanquet, J. 1933. L'association végétal climatique et le climax du sol dans le Midi méditerranéen. Bull. Soc. Bot. de France 80: 715-722.
- . Plant sociology. 1932. Transl., rev., & ed. by G. H. Fuller and H. S. Conard. McGraw-Hill. New York.
- Butler, B. S., et al. 1920. Ore deposits of Utah. U. S. Geol. Surv. Prof. Paper 111.
- Cain, S. A. 1944. Foundations of plant geography. Harpers. New York.
- . 1947. Characteristics of natural areas and factors in their development. Ecological Monog. 17: 185-200.
- Cooper, W. S. 1926. The fundamentals of vegetation change. Ecology 7: 391-413.
- . 1939. Fourth expedition to Glacier Bay, Alaska. Ecology 20: 103-155.
- Crocker, R. L., and J. G. Wood. 1947. Some historical influences on the development of the South Australian vegetation communities and their bearing on concepts and classification in ecology. Trans. Roy. Soc. South Australia 71: 91-136.
- Du Rietz, G. E. 1950. Guide for Excursion C III c, 7th International Bot. Cong., Stockholm.
- Ellison, L. 1943. What is range improvement. Ames Forester 31: 15-22.
- . 1947. Subalpine vegetation of the Wasatch Plateau, Utah. Ph.D. Thesis. Univ. of Minnesota.
- Etter, H. 1947. Ueber die Waldvegetation am Südostrand des schweizerischen Mittellandes. Mitteil. Schweiz. Anstalt für das forstliche Versuchswesen 25: 137-210.
- Feher, D., and M. Frank. 1945/46 (1947). Researches on the geographic distribution of the mikroflora. Erdeszeti Kiserletek 46: 299-337.
- Hall, E. H. 1946. Mammals of Nevada. Univ. of California Press. Berkeley.
- Iaroshenko, P. D. 1946. [On changes in the plant cover.] Bot. Zhurnal SSSR 31: 29-40.
- Ives, R. L. 1941. Forest replacement rates in the Colorado headwaters area. Bull. Torrey Bot. Club 68: 407-408.
- Jenny, H. 1930. Study of the influence of climate on the nitrogen and organic matter content of the soil. Missouri Agric. Exp. Sta. Res. Bull. 152.
- . 1941. Factors of soil formation. McGraw-Hill. New York.
- . 1946. Arrangement of soil series and types according to functions of the soil forming factors. Soil Sci. 61: 375-391.
- Leuenberger, R. 1950. Beitrag zur Kenntnis der Humuskarbonatböden und Rendzinen im Schweizer Jura. Juris Verlag. Zurich.
- Lüdi, W. 1932. Die Methoden der Sukzessionsforschung in der Pflanzensoziologie. In E. Abderhalden, Handbuch der biologischen Arbeitsmethoden. Abt. XI, Methoden zur Erforschung der Leistungen des Pflanzenorganismus. Teil 5, Pflanzengeographische Oekologie. Pp. 527-728. Urban & Schwarzenberg. Vienna.
- Munns, E. N., chairman of committee. 1950. Forestry terminology, revised edition. Soc. Amer. Foresters. Washington, D. C.
- Pallmann, H., F. Richard, and R. Bach. 1948. Über die Zusammenarbeit von Bodenkunde und Pflanzensoziologie. 10th Congress des Internationalen Verbandes forstlicher Versuchsanstalten, pp. 53-95.
- Ramaley, F. 1931. The vegetation of the chaparral covered foothills southwest of Denver, Colorado. Univ. Colo. Studies 18: 231-237.
- Salisbury, E. J. 1942. The reproductive capacity of plants. Bell and Sons. London.

- Sampson, A. W.** 1919. Plant succession in relation to range management. U. S. D. A. Bull. 791.
- Shreve, F.** 1915. Vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. of Washington Pub. 217.
- Sukachev, V. N.** 1944. [On the principles of a genetic classification in biocoenology.] Zhurnal Obschchei Biology 5: 213-225.
- Tansley, A. G.** 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.
- Thorntwaite, C. W.** 1948. An approach to a rational classification of climate. Geog. Rev. 38: 55-94.
- Tüxen, R.** 1931/32. Die Pflanzensoziologie in Forschung und Lehre. II. Die Pflanzensoziologie in ihren Beziehungen zu den Nachbarwissenschaften. Der Biologe 1: 180-187.
- Tüxen, R., and H. Diemont.** 1937. Klimaxgruppe und Klimaxschwarm. Jahresbericht Naturhist. Gesell. Hannover 88/89: 73-87.
- Van Burkalow, A.** 1945. Angle of repose and angle of sliding friction. Bull. Geol. Soc. Amer. 56: 669-707.
- Vilensky, D. G.** 1937. [On some regularities in the development of processes of soil formation.] Pochvovedenie 1937: 792-809.
- Weaver, J. E.** 1924. Plant production as a measure of environment. Jour. Ecology 12: 205-237.
- Whiteside, E. P., and C. E. Marshall.** 1944. Mineralogical and chemical studies of the Putnam silt loam soil. Missouri Agric. Exp. Sta. Res. Bull. 386.

THE AUTOTREPHON: AN APPARATUS FOR REARING INSECTS UNDER CONTROLLED CONDITIONS WITH AUTOMATIC TIME-CONTROLLED WITHDRAWAL OF SAMPLES¹

JOHN STANLEY

Department of Zoology, McGill University, Montreal, Canada

INTRODUCTION

The writer has been interested for some years in the problem of the assessment of the suitability of a given set of environmental conditions for the growth and development of stored-products insects. A previous paper (Stanley 1946) develops the concept of an "Environmental Index" which has a value of 0 when the environment is lethal, and a value of 1.0 when the environment is optimal.

In order to obtain tabulated values of this Index for a range of conditions and insect species, it is necessary to carry out a very large number of rearings. This poses some severe problems because growing insects pay no attention to working hours or to days of the week. Samples for study must be taken at times which are often very inconvenient unless the laboratory can afford the luxury of a staff on 24-hour duty.

Long experience with cultures of *Tribolium confusum* brought the writer to the belief that the data obtained from a replicated series of cultures (each examined once) would not be significantly less reliable than those from a single culture repeatedly examined. If, then, one sets up as many replicates as one proposes to make examinations, examines each one at an appropriate time and then discards, one substitutes the variance between cultures for that between examinations, and this does not seriously increase the total variance of the data.

Such a technique makes it possible to solve the sampling problem mechanically,

¹ Excess costs occasioned by the length and complexity of this paper have been met by a grant from the McGill University Research Fund.

if some means can be devised to withdraw the successive replicates from the rearing chamber and transfer them to a cool storage chamber (below the minimum effective temperature). In storage, no growth will occur, and the stored samples can wait until it is convenient to examine them. Such an apparatus has been designed and built in the Department of Zoology at McGill University, and a brief description follows. The apparatus is of considerable complexity and a complete description of every detail would be impossible in the space available. Should any laboratory wish to duplicate this apparatus, the writer will be pleased to give additional details and advice.

A suitable name for the apparatus presented a problem. The name "Autotrephon" was finally worked out with the kind assistance of Professor W. D. Woodhead, Chairman of the Department of Classics at McGill University. The name is derived from the *τρεφον*, a nurse.

THE APPARATUS

General form of the apparatus

A general view of the apparatus is shown in Figure 1 and a plan-view diagram in Figure 2. The latter shows also the lines of sight of the photographs which form the majority of the figures of this paper. The arrows indicate direction, and the relative breadth of each arrow indicates the height above floor level of the line of sight. Thus, arrows tapering to a slender point slope down, and *vice versa*.

The apparatus consists of a chamber (WC, Figs. 1, 2, 3), controlled for temperature and relative humidity as de-

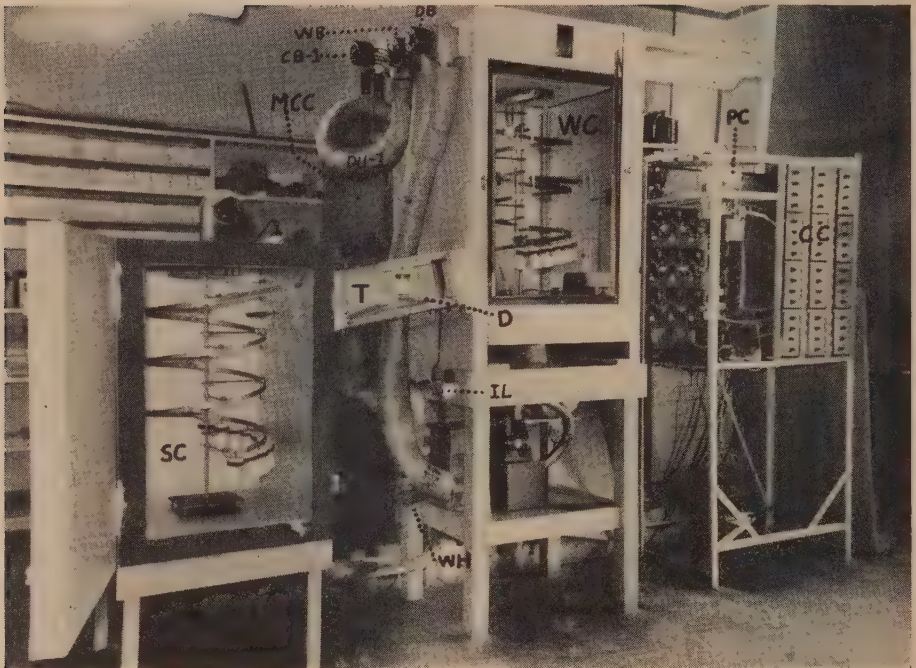


FIG. 1. General view of the apparatus from the front. CB-1, cooling blower; CC, control console; D, doors in tunnel; DB, drying blower; IL, indicator light of humidifier heater; MCC, main cooling chamber; PC, program controller; SC, cool storage chamber; T, tunnel between warm and cool chambers; WB, wetting blower to humidifier; WC, warm chamber; WH, heater for humidifier.

scribed below. This chamber is connected by a tunnel (T, Figs. 1, 2, 16, 17, 18), closable by doors (D, Figs. 1, 16), to a cool storage chamber (SC, Figs. 1, 2, 8, 16, 19). The replicated cultures are housed in plastic vials (V, Figs. 3, 19) hung from monorail hangers on a helical monorail track (HT, Figs. 1, 3, 13, 19). The series of vials is held back by an escapement (E, Fig. 3, and Fig. 13). At the moment of sampling, as determined by a program controller (PC, Fig. 1, and Figs. 14, 15, 20), this escapement slips the lowest vial of the series and allows it to run by gravity through the tunnel into the storage helix in the cool chamber (shown in greater detail in Fig. 19). The doors of the tunnel open and close automatically as the sample passes through. After sampling, the whole series of vials moves down one place, and the next

sample-vial comes into the escapement, ready to be released at the next sample-hour.

The program controller, as described below and shown in Figures 14 and 15, is completely flexible and can be pre-set to slip samples at any hour, and a program covering as much as 72 hours can be set into it. In actual practice, the operator decides on the basis of some rough studies as to the hours at which samples are to be drawn. This program may cover perhaps months of time. He sets the first part of it (up to 72 hours) into the controller, and feeds in additional portions as the controller works through what has been given to it. Meanwhile he removes and studies the samples as they accumulate in the storage helix. It is to be emphasized that the controller places no restrictions at all on the operator as to the

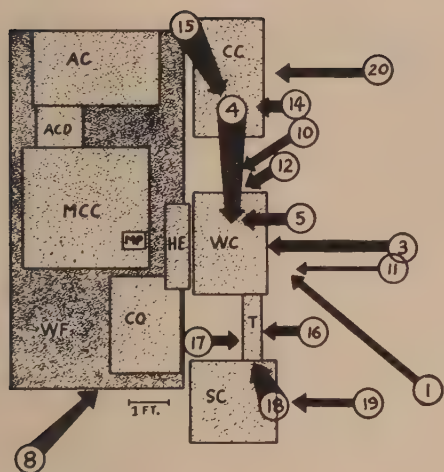


FIG. 2. Plan-view diagram of apparatus, showing lines of sight (photographs and drawings for the other figures). Thick arrows denote a high line of sight, arrows tapering to the tip denote a downward line of sight. AC, auxiliary chambers for rearing (not described in this paper); ACD, cooling ducts for auxiliary chambers; CC, control console; CO, refrigeration compressor; HE, heat exchanger; MCC, main cooling chamber; MP, motor of circulation pump for heat exchanger water; SC, cool storage chamber; T, tunnel from warm chamber to cool storage chamber; WC, warm chamber; WF, heavy wooden foundation for heavier parts of apparatus.

nature of the program. Samples can be withdrawn every hour or at any other interval, or at varying intervals, mixed up together in any way whatever as shown in Tables II to VII. By a simple change of parts, the minimum sampling interval can be changed from one hour to any other period less than an hour. So far, however, it has not seemed necessary to sample more often than once per hour. A program once decided upon is in no way fixed, but can be altered at will. The program controller is described in detail later.

Details of parts of the apparatus

The warm chamber. This chamber was built by extensive modifications of a Cenco Forced Circulation, Metal Cabinet Incubator (Cenco Cat. No. 46023). This in-

cubator has a triple wall, the laminae of which for purposes of reference may be called outer, middle and inner. The air in the incubator is continuously withdrawn from the inside by a sirocco-type blower (SB, Fig. 3) located in the center of the roof. The air passes radially in a roof-space between the inner and middle laminae of the roof (see Fig. 7), descends down the sides of the incubator between the inner and middle laminae, entering the inside space of the incubator again at the bottom of each side. It so enters through a slot which results from the fact that the inner lamina stops short about 1 inch from the floor (S, Fig. 3). The incubator as delivered had no insulation between the outer and middle laminae. This space was filled with rock-wool and, as a further insulation, blocks of "Ten-Test" (a patented wood-fibre wall board $\frac{1}{2}$ inch thick) were piled up around the blower-motor on the roof (B and SBM, Figs. 4, 7). In these figures, much of the roof insulation has been removed for purposes of clarity in the illustrations. Ducting and additional blowers were then installed to effect cooling, wetting and drying of the contained air, as needed (Figs. 1, 4, 7, 8, 10, 11, 16).

Heating system of the warm chamber.

This is controlled by one side-contact of a special DeKhotinsky Bimetallic Thermostat (Cenco Cat. No. 99015) rendered more sensitive by the addition of two more bimetallic helices (Cenco Cat. No. 99110) in series with the one provided. Referring to Figure 5 and to TH-1, Figure 3, the center-rod, CR, was lengthened, and any possible sag of the triple helix supported by annular spacing rings (SR, Fig. 5) fitting inside the helix and over the center-rod. The outer end of the center-rod rests in a bronze bearing (BE, Fig. 5) and the opposite end passes as usual in these thermostats, through the wall to the operating head of the instrument (see Fig. 12). The bearing BE is held in a cut-away supporting tube (ST, Fig. 5). The "hot" side of the double set of contacts controls a 100-watt chromel

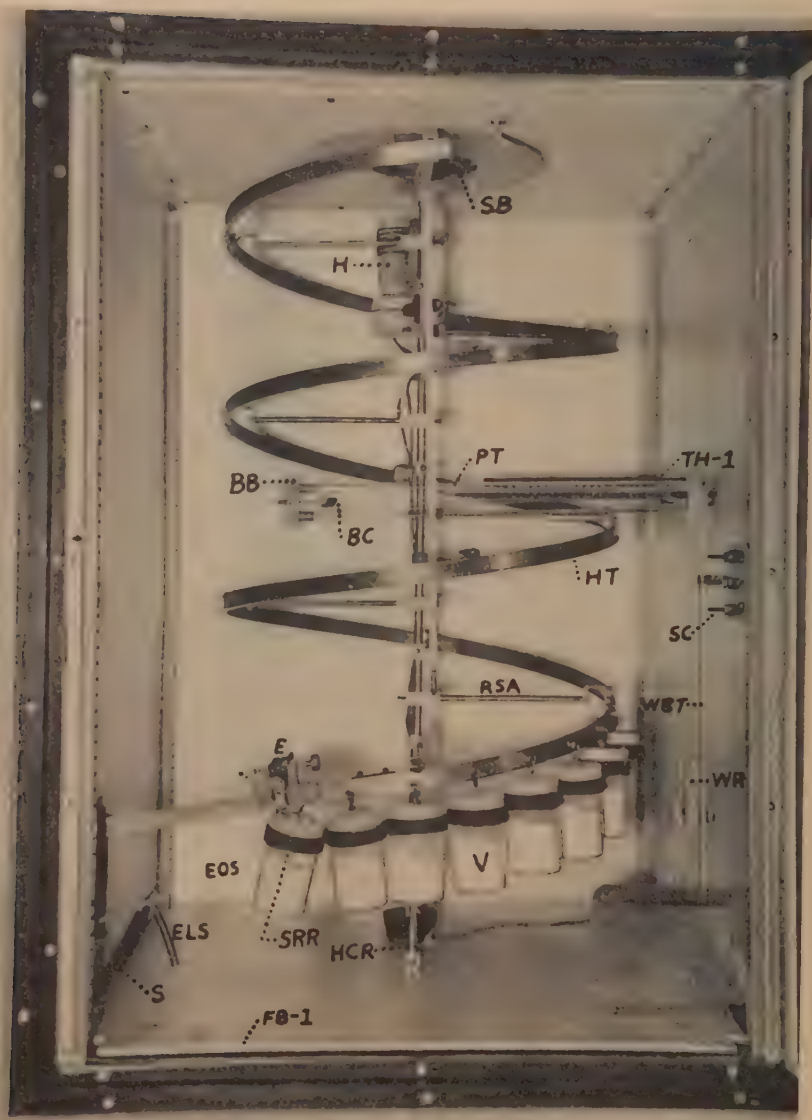


FIG. 3. Inside view of warm chamber. BB, brass bridge forming end of frame of humidistat; BC, bakelite clip holding one end of hairstrand of humidistat; E, escapement; ELS, spring for escapement-operating string; EOS, escapement-operating string; FB-1, floor baffle; H, chromel-wire heater; HCR, central support rod of helix; HT, helical track; PT, pyrex tube forming side of humidistat frame; RSA, radial supporting arm of helix; S, slot through which continuously re-circulated air enters chamber; SB, sirocco-type blower rotor; SC, spare 6-volt connectors; SRR, soft rubber anti-squeeze rings on vials; V, sample vials; WBT, wet-bulb thermometer; WR, water reservoir for wet-bulb thermometer.

wire heater coil (H, Fig. 3) placed below the air exit in the roof of the chamber. It controls via a Silent Power Relay (American Instrument Co., Cat. No. 4-371A) located in the control console (CC, Figs. 1, 2 and Fig. 20). The original large heating coils, along with their thermostat and all associated wiring and controls were removed from the roof-

space. Sharpened in this way, control is effective to $\pm 0.1^\circ \text{C}$., with fluctuations of about 0.2°C ., when the humidity controls operate. It was found advisable to replace the original contacts of this thermostat with pure silver blocks to prevent sticking on the 6-volt D.C. controlling current.

Cooling system of the warm chamber.

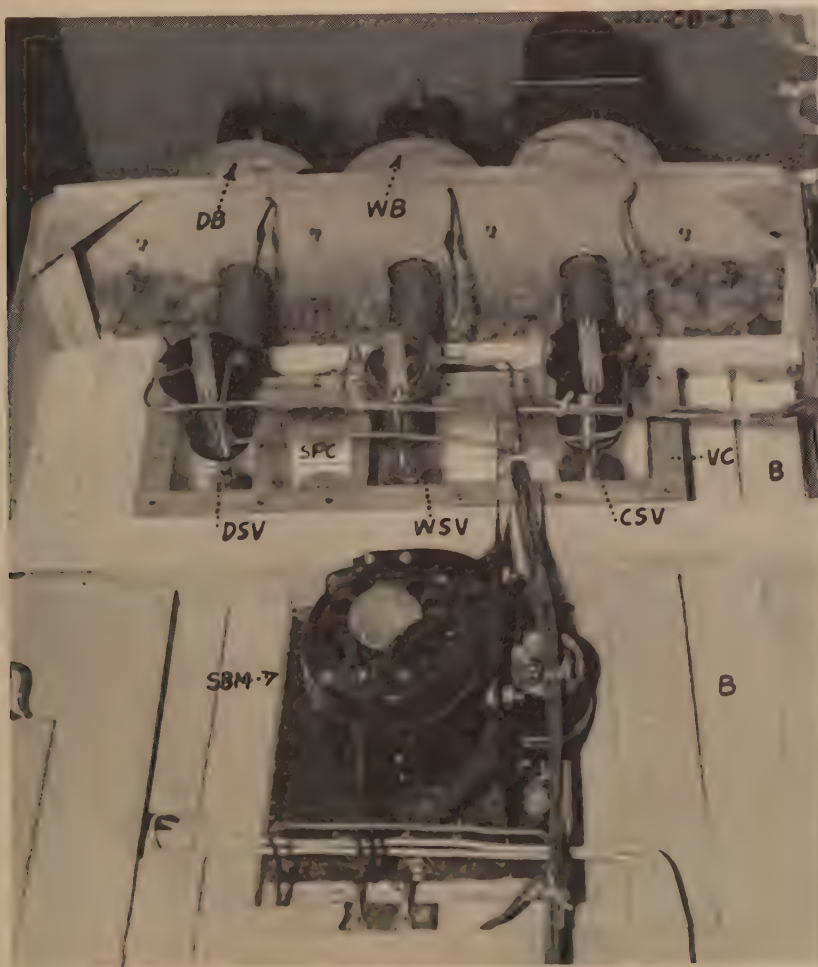


FIG. 4. View of top of warm chamber. B, insulating blocks of "Ten-Test," most of which have been removed for clarity. Normally they cover the pipes between the valve chest and the blowers; CB-1, blower for cooling system of warm chamber; CSV, solenoid valve of cooling system; DB, blower of drying (de-humidifying) system of chamber; DSV, solenoid valve of de-humidifying system; SBM, motor of stroco-type blower (main circulation blower); SPC, spare compartment in valve chest; VC, valve chest; WB, wetting (humidifying) blower; WSV, solenoid valve of humidifying system.

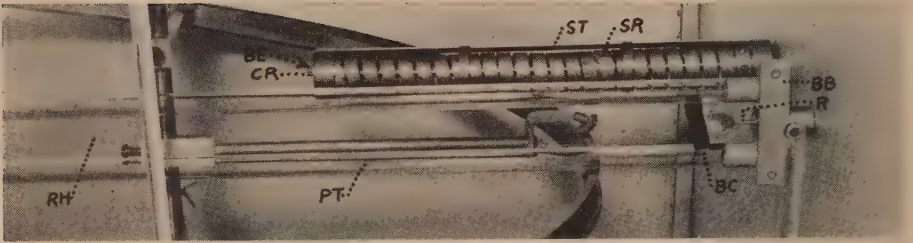


FIG. 5. Detail view of thermostat and humidistat of warm chamber. BB, brass bridge forming end of frame of humidistat; BC, bakelite clip holding end of hair strand; BE, end-bearing of actuating rod of thermostat; CR, center or actuating rod of thermostat; PT, pyrex tube forming side of frame of humidistat; R, rod going through wall of chamber to head of humidistat, appearing again outside in Figure 12; RH, strand of human hair; SR, supporting ring joining successive lengths of bimetallic helix, and bearing internally on the center rod; ST, slotted tube supporting the supporting rings and end-bearing of the thermostat center rod.

This system is controlled by the "cold" side of the above thermostat which, via another Silent Power relay, controls a blower (CB-1, Figs. 1, 4, 7, 8) which passes air from the roof-space of the chamber through a heat-exchanger (HE, Figs. 1, 2, 8, and Fig. 9) back to the warm chamber. This exchanger (described in detail below) is adjusted so that its cooling surfaces are about $\frac{1}{2}^{\circ}$ C. above the dew-point of the air in the warm chamber.

Thus there is little loss of moisture from this air. Control by cooling is not quite as good as by heating, but is accurate to about 0.2° C. Unless care is taken with the setting of the heat-exchanger temperature, cooling affects the humidity control, and in some cases a type of cyclical hunting has developed between the wetting, drying, cooling and heating systems. This has always been preventable by adjustment of the heat-exchanger temperature

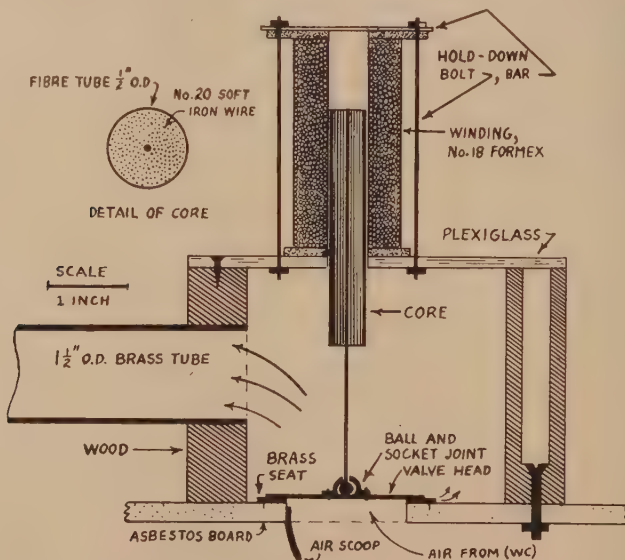


FIG. 6. Diagrammatic vertical section of valve chest and any one of the three solenoid valves. The valve is shown closed.

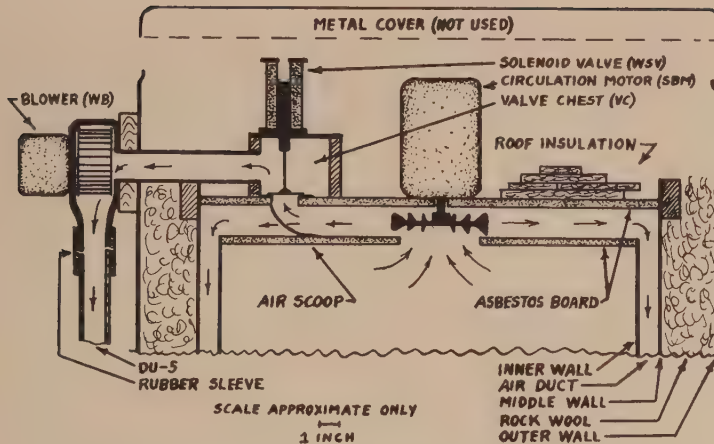


FIG. 7. Diagrammatic vertical section of the upper part of the warm chamber, showing the relation of valves, blowers and air passages. This is only approximately to scale, and details are diagrammatic, as it was not possible to disassemble for exact detail. The two motors shown are not sectioned.

and the differentials of the thermostat and humidistat of the warm chamber, and has never been a serious problem.

In detail, when there is a demand for cooling, the thermostat TH-1 (Fig. 3) closes on the cold side, energising a Silent Power relay. This delivers 110-volt A.C. power to the cooling blower (CB-1, Figs. 1, 4, 8) and, via a resistance to a solenoid valve (CSV, Figs. 4, 7 and Fig. 6) opening the latter. Air is thus drawn from the valve-chest (VC, Figs. 4, 7) and driven through a flexible duct (DU-1, Figs. 1, 8) to the heat-exchanger (HE, Figs. 1, 2, 8 and Fig. 9). This air passes through the tubes of the exchanger, is cooled, and passes back to the warm chamber via another duct (DU-2, Figs. 10, 11) to enter the warm chamber underneath a floor baffle (FB-1, Fig. 3). This baffle is located 0.75 in. above the floor of the chamber, and extends to within 1 in. of the wall all round. Thus the incoming air mixes with the air passing down the side passages from the circulation blower, and the whole mass of air is thrown into the incubator space with marked turbulence. This results in a very even temperature throughout the space. Variations are nowhere more than $0.2^{\circ}\text{C}.$, and

are almost perfectly uniform around the helix and the samples.

When cooling is sufficient, the blower stops and the solenoid valve closes. The purpose of the valve is to prevent thermosiphoning when cooling is not required. In Figure 4, it would appear that the coils of the solenoid valves are suspended in space. This is because the top of the valve-chest is made of transparent plastic which does not show in the photograph. The small compartment, SPC, in the chest between DSV (drying solenoid valve) and WSV (wetting solenoid valve) is for another valve, should it ever be needed. A diagrammatic longitudinal section of a valve is shown in Figure 6, and of the roof of the warm chamber and its air passages in Figure 7.

The solenoid valves and associated structures: It is necessary to close off the air passages through the humidifier, cooler and de-humidifier when these conditioners are not operating, or the small positive pressure built up in the roof air-space will force a current of air through all these units, resulting in much waste conditioning. The solenoid valves, of which there are three, perform this function.

The three identical valves are held down

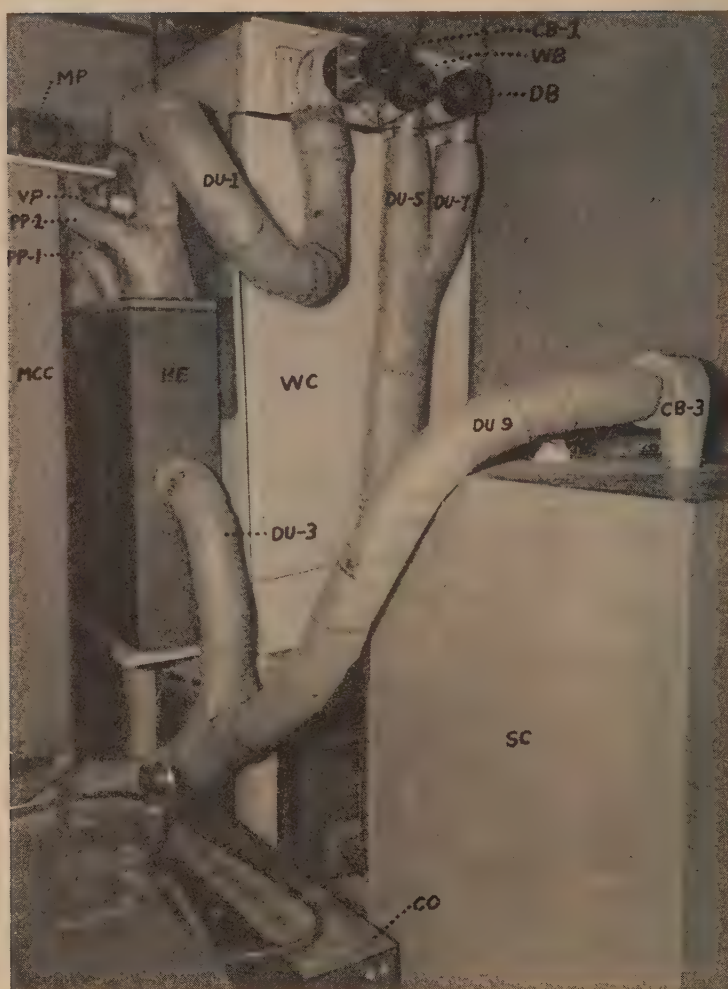


FIG. 8. View of left end of apparatus. CB-1, blower of cooling system of warm chamber; CB-3, blower for cooling cool storage chamber; CO, refrigeration compressor; DB, de-humidifying blower for warm chamber; DU-1, air duct from warm chamber to heat exchanger, for cooling; DU-3, air duct from air space of heat exchanger, back to main cooling chamber, carrying air which has cooled water tank of exchanger; DU-5, air duct from warm chamber to humidifier; DU-7, air duct from warm chamber to de-humidifier; DU-9, air duct from main cooling chamber to blower for cooling the cool storage chamber (the return duct back to the main cooling chamber is underneath, and cannot be seen); HE, heat exchanger; MCC, main cooling chamber; MP, motor driving circulation pump for water in copper tank of heat exchanger; PP-1 pipe from copper tank of heat exchanger to circulation pump; PP-2, return pipe from pump to copper tank; SC, cool storage chamber; VP, vane pump which circulates water in copper tank of heat exchanger; WB, blower for humidifying system of warm chamber; WC, warm chamber.

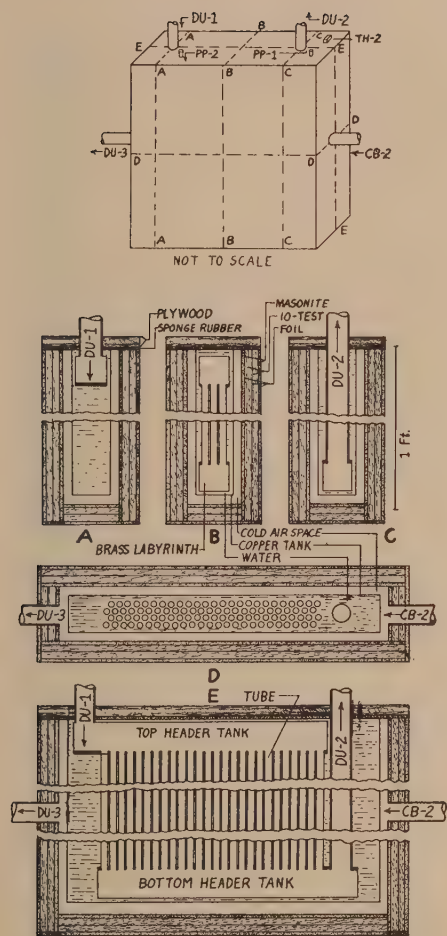


FIG. 9. Diagrammatic sections to show details of construction of the heat exchanger (only approximately to scale). A, B, C, D and E of the upper figure show the planes of section for the other figures. CB-2, short duct from cooling blower, forcing cold air from main cooling chamber to air space around copper water-tank; DU-1, air duct leading air (to be cooled) from warm chamber to exchanger labyrinth; DU-2, return air duct from labyrinth to warm chamber, carrying air which the exchanger has cooled; DU-3, return air duct from air-space around copper tank of exchanger, back to main cooling chamber, returning air which has cooled the water tank; PP-1, pipe from copper water tank of exchanger to circulation pump; PP-2, return pipe from pump to water tank; TH-2, thermostat controlling temperature of water in copper tank. NOTE: for clarity, only three rows of brass tubes are shown between the header tanks in

by bolts to the plexiglass roof of the valve chest as seen in Figures 4, 6 and 7, with their respective stems and heads hanging down each in a separate compartment of the valve chest (see Fig. 4). In the closed condition, the head lies over a brass annular valve seat screwed onto the floor of each compartment, around the port opening into the compartment from the the roof air-space, thus sealing these ports.

When energized by current from the relay (which also operates the associated blower), the solenoid winding (No. 18 Formex insulated wire on a bakelite spool) lifts the core with attached stem and head, and opens the valve. The core consists of a thin-walled fiber tube ($\frac{1}{2}$ in. outside diameter) tightly packed with No. 20 soft iron wire, and impregnated with "Dekad-hese" cement (a patented cellulose-acetate-like office adhesive). The valve stem is inserted in the tube, and the wire packed in around it. No stems have ever come loose. The head is a flat brass disc 1.75 in. diameter held to the stem by a ball-and-socket universal joint permitting some movement to allow for inaccuracies in the set of the valve as it falls closed. (This joint must be firm and strong as the valves operate some thousands of times per day, and there is much pounding.) The valves operate on 115 volts A.C., with a resistance (not shown) in series, so that lifting is quick, but overheating is avoided. (For the windings as shown in Figure 6, about 150 ohms is needed for 115 volts, A.C.)

The heat-exchanger in detail. The need for a heat-exchanger arises from the fact that if the air from the warm chamber were passed directly to the main cooling chamber (MCC, Figs. 1, 2, 8), not only would the rate of cooling be too great for accurate control, but moisture would freeze out on the main cooling coils, clogging them and interfering with humidity control in the warm chamber. By setting the surfaces of the exchanger at about $\frac{1}{2}^{\circ}$

Figures 9B and 9E. Figure 9D shows the actual construction.

C. above the dew-point of the air in the warm chamber, these difficulties are avoided.

The heat-exchanger (HE, Figs. 1, 2, 8 and in detail in Fig. 9) consists of an insulated box 27 in. long, 27 in. high and 7 in. thick (outside), with walls $1\frac{3}{8}$ in. thick. The walls consist of the following layers from the outside inward; Masonite, aluminum foil, "Ten-Test," aluminum foil, "Ten-Test," aluminum foil, Masonite. Inside this insulating jacket is a watertight copper tank 23 in. long, 23 in. deep and 3 in. wide. There is thus an air space of about $\frac{5}{8}$ in. on the sides and bottom between this tank and the jacket.

The copper tank is filled with water, and contains the brass cooling labyrinth. This consists of a top and bottom header-tank each 21 in. long, 2 in. deep and $2\frac{1}{2}$ in. wide, made of heavy brass sheet. The top of the bottom tank and the bottom of the top tank are of $\frac{1}{4}$ in. brass, each drilled with some 125 holes $\frac{1}{2}$ in. in diameter. The two tanks are joined vertically by a forest of 125 brass tubes each 18 in. long, sweated into the holes in the heavy plates of the header-tanks. The internal spaces of this radiator-like structure communicate with the warm chamber via the flexible ducts DU-1 (Figs. 1, 8) and DU-2 (Figs. 10, 11).

The water in the copper tank is continuously circulated by a small vane pump (VP, Fig. 8) driven by a $\frac{1}{6}$ H.P. motor on top of the main cooling chamber (see MP, Figs. 2, 8). This pump draws about 6 gallons of water per minute from the bottom at one end of the tank via the pipe PP-1 (Fig. 8) and discharges it at the surface at the other end via the pipe PP-2.

The operation of the heat-exchanger is as follows: controlled by a DeKhotinsky bimetallic thermostat (TH-2, Fig. 9, Cenco Cat. No. 99005) which dips into the water in the copper tank, the blower CB-2, (Fig. 10) draws air from the main cooling chamber and blows it through the air space around the copper tank back to the main cooling chamber via the duct DU-3 (Fig. 8). A Silent Power relay is

interposed in this circuit. This controlled air-flow cools the water in the tank as needed. Air to be cooled passes through the labyrinth as previously explained. A small drain pipe from the labyrinth carries any condensed moisture to the humidifier (HU, Fig. 11). As this pipe has an in-

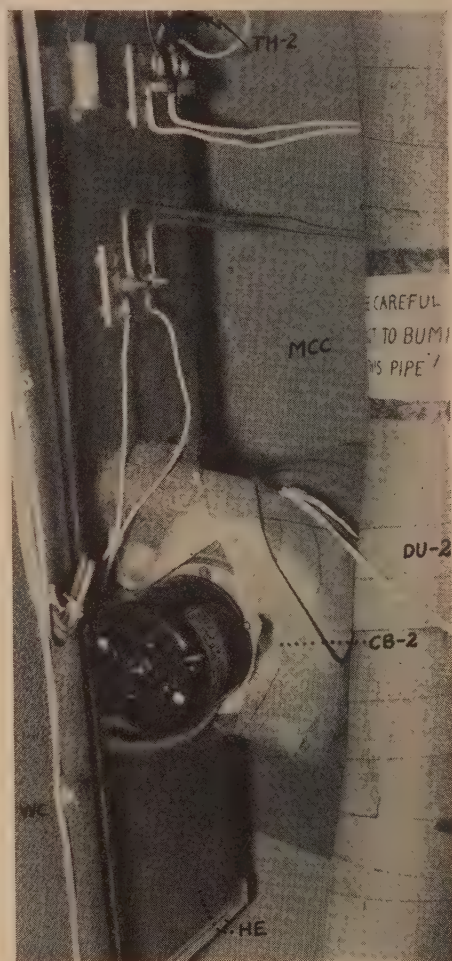


FIG. 10. View of right end of heat exchanger. CB-2, blower forcing cold air from main cooling chamber to air space around copper watertank in heat exchanger; DU-2, air duct carrying cooled air from labyrinth of heat exchanger to warm chamber; HE, heat exchanger; MCC, main cooling chamber; TH-2, thermostat (not visible), controlling temperature of water in copper tank of exchanger; WC, warm chamber.

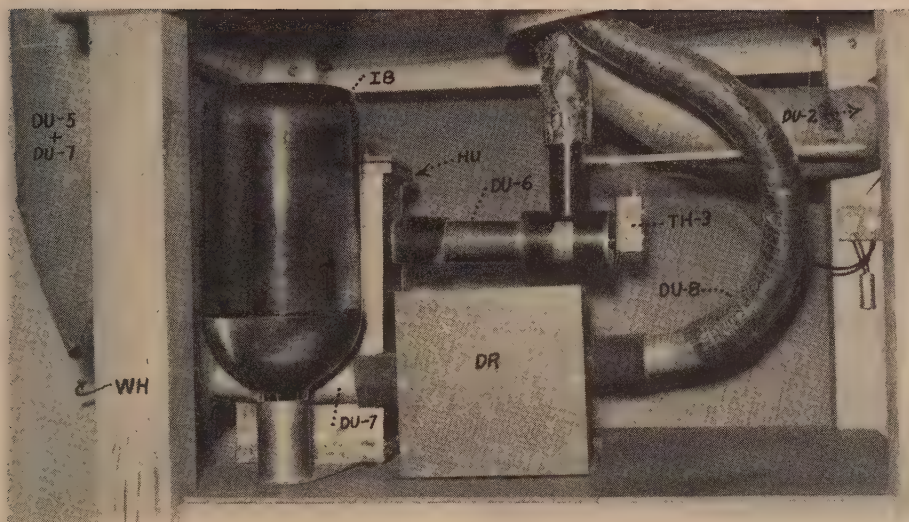


FIG. 11. View of humidifier, etc., underneath warm chamber, seen from the front. DR, de-humidifier for warm chamber; DU-2, air duct carrying cooled air from labyrinth of heat exchanger to warm chamber; DU-5 + 7, air ducts bound in common casing, DU-5 being from warm chamber to humidifier, DU-7 from warm chamber to de-humidifier; DU-6, air duct from humidifier to warm chamber, carrying wetted air; DU-8, air duct from de-humidifier to warm chamber, carrying dried air; IB, inverted water bottle holding water for humidifier wicks; HU, humidifier; TH-3, thermostat controlling humidifier heater coil (WH), and thus the temperature of the wetted air going to the warm chamber; WH, heater (not visible), for heating air going to humidifier. (Can be seen in Fig. 1.)

ternal diameter of only $\frac{1}{8}$ in., the air-loss through it is negligible.

The high heat-capacity of the water in the copper tank damps out any fluctuations, and provides a reserve of cooling. The cooling is very effective. Air admitted to the exchanger at 35°C . leaves it at about 10°C . with the exchanger set at 10°C . With the main cooling chamber at -5°C ., the water in the exchanger tank can be frozen. The air in duct DU-3 gains about 1° to 1.5°C ., due to friction and conduction from the walls. While cooling of the warm chamber has proved adequate under most conditions, some difficulty has arisen when the room is unusually warm, the warm chamber is set well below room temperature, and the relative humidity in the warm chamber is high, say, 80 per cent. Under such conditions, it is necessary to set the exchanger below the dew-point of the warm air, and some water is lost. This results

in a fall of the wet-bulb temperature in the warm chamber of as much as 0.5 to 0.75°C . when the cooler operates, with recovery in about 45 seconds. The difficulty has been obviated by arranging forced circulation of air in the laboratory, under the control of an input fan and thermostat in the window. This removes by-product heat from the many motors and lowers the room temperature.

Humidification and de-humidification.

Both humidification and de-humidification are controlled through the two sides of a single-contact, double-throw humidistat (HS, Fig. 3 and Figs. 5, 12), operating through two Silent Power relays, to control solenoid valves and blowers. The blowers pass air from the warm chamber through a wetter or dryer as needed, in exactly the same manner as is done for cooling. Wetted or dried air returns to the warm chamber underneath the floor baffle (FB-1, Fig. 3).

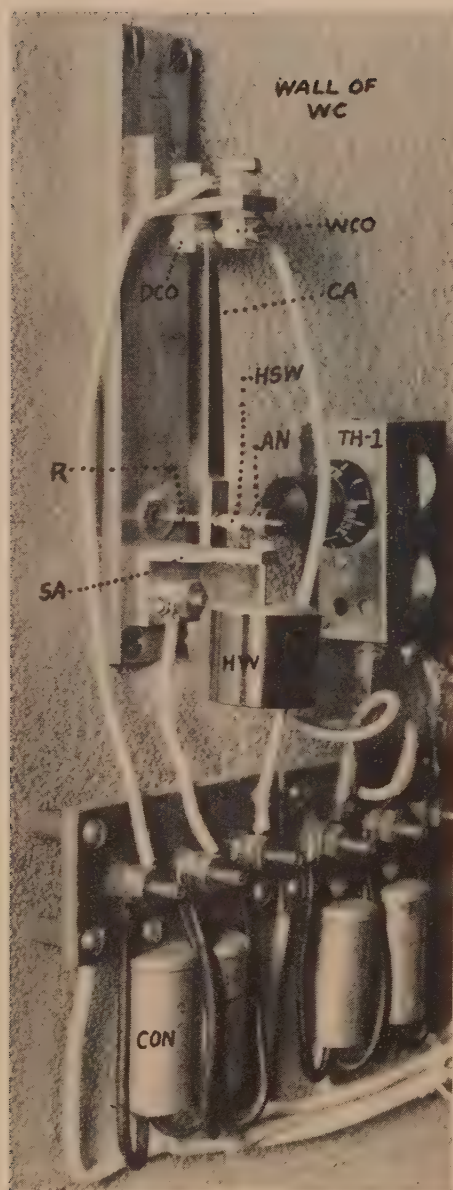


FIG. 12. View of heads of thermostat and humidistat of warm chamber, on right end of chamber, outside. AN, fine adjustment nut for setting humidistat; CA, contact arm of humidistat, moved by pull of hair strand; CON, anti-sparking condensers; DCO, "too dry" contact of humidistat (as hairs shrink when air in warm chamber is too dry, CA makes contact with DCO and turns on humidifying blower via a

The humidifier. This consists of a chamber made of sheet brass, 6 in. square and 13 in. high (HU, Fig. 11) containing about 100 feet of $\frac{1}{2}$ -in. wide lamp-wicking wound in staggered rows on a removable brass framework. Under the control of the humidistat (HS, Fig. 3), the wetting blower (WB, Figs. 1, 4, 8) draws air from the valve-chest (VC, Figs. 4, 7) through the solenoid valve (WSV, Fig. 4), and forces it via duct DU-5 (Figs. 8, 11) to the humidifier. Here it picks up moisture, and returns to the warm chamber beneath the floor baffle, via duct DU-6 (Fig. 11). Water is supplied to the humidifier from an inverted bottle (IB, Fig. 11) which maintains a pool in the bottom of the humidifier.

It is necessary to supply energy for evaporation of the water, otherwise the humidifier cools, and the humidity in the warm chamber will not go higher than a value determined by the warming of saturated air from the cold humidifier. This heat is supplied by a 150-watt chromel wire heater (WH, Figs. 1, 11), set into duct DU-5 just ahead of the humidifier. It is controlled by the DeKhotinsky thermostat TH-3 (Fig. 11) inserted in the efferent duct from the humidifier (DU-6, Fig. 11). This thermostat controls the heater through a Silent Power relay so connected to the relay of the wetting-blower that heat for the humidifier cannot be supplied unless the wetting-blower (WB, Figs. 1, 4) is spinning. When this blower is operating, the heater is autonomous. Thus, the humidified air leaves the humidifier at the same temperature as the warm box. Control is to about $\pm 0.2^\circ$ C., wet-bulb temperature. A small neon pilot light connected across this

relay); HSW, hardened steel wedge transferring pull of hair strand to contact arm (CA); HW, weight stretching hair strand; R, actuating rod from end-clip of hair strand through wall to contact arm; TH-1, thermostat head of warm chamber, controlling heating and cooling; WCO, "too wet" contact of humidistat, is contacted by CA if air in warm chamber is too wet, expanding hair strand.

heater facilitates the setting of the thermostat TH-3 by indicating when the coil is heating. (See IL, Fig. 1.)

De-humidification is effected by blowing air in a similar way through a drier (DR, Fig. 11) containing silica gel in shallow trays. It has never been used, as the air in Montreal is always drier than the warm chamber in winter, and the laboratory does not operate in July and August. It has occasionally "fired" to repress an overshoot on the humidification system, and seems effective. It is connected to the warm chamber via solenoid valve DSV, blower DB, duct DU-7, and return via DU-8.

The humidistat. Commercial humidistats of the hair-type proved to be complete failures for this application, and other types were too expensive and cumbersome. Through the kindness of the Director of the Dominion Parasite Laboratory, Belleville, Ontario, the writer was able to examine a successful hair-humidistat used there. It was subsequently re-designed for use in this equipment.

Referring to Figure 3 and in detail to Figure 5, two pyrex-glass tubes PT, with two brass end-bridges BB, form a supporting frame for the ribbon of hairs RH. The ribbon consists of 25 blonde human hairs; 12 in. long, fastened at each end into a bakelite clip BC. The hairs were fastened to one clip, stretched evenly by hanging lead shot on them, and then cemented into the other clip. The ribbon being $1\frac{1}{4}$ in. wide, the inter-hair spacing is approximately .05 in., and each hair is well exposed to the ambient air. The left-hand clip is fastened via a ball-and-socket joint to a support rod passing through one bridge, with an adjusting nut, N, on the end. Rough adjustments of ribbon-position are made here. The right-hand clip fastens via a ball-and-socket joint to the operating rod which passes through the other bridge and the chamber wall and appears at the control head of the humidistat as at R (Figs. 5, 12).

Referring to Figure 12, the phosphor-

bronze spring contact arm CA pivots about a fine steel axle SA, and tension is maintained on the hair ribbon by the weight HW, loosely fastened to the right-angle extension of the contact arm. The weight weighs 125 grammes, giving a computed tension on the ribbon of about 250 grammes. The contact arm pulls the rod R via a hardened steel wedge HSW, bearing in a tiny vee-groove in the contact arm. The wedge is honed to a very sharp edge, and provides a frictionless joint showing no "set." (A ball-and-socket joint here produced friction and jerky movement of the arm, so that control proceeded by jumps.) Fine control of the humidistat-setting is through the adjustment nut AN (Fig. 12) and is effective to $\pm 0.2^\circ$ C., wet bulb. The contacts are pure block silver, one domed, the other flat. With weekly polishing, they have given no trouble with sticking on the 6-volt D.C. controlling current. CON of Figure 12 are Stromberg-Carlson .02-mfd. condensers, Type 21535, for spark suppression at the humidistat and thermostat contacts.

This humidistat controls very well, for the following reasons: (a) the hairs are quite long, (b) they are spaced wide apart, and each is fully exposed to the air, (c) each hair is under the same tension, (d) the tension on the hair ribbon is substantially equal for all settings, and is low in any case, (e) the pyrex rods and brass used in construction eliminate warping from temperature or humidity changes, (f) the use of the steel wedge to move the switch arm eliminated friction.

The instrument shows little or no creep, the wet-bulb temperature (corrected for barometer) showing a random variation of only 0.1 to 0.2° C. per day after days of control. Variations of wet-bulb temperature of as little as 0.1° C. are easily made, and the control stays within 0.5 per cent of the set value over wide forced variations of temperature ($\pm 10^\circ$ C.). It will also return to within $\frac{1}{4}$ of 1 per cent of the correct setting if the relative humidity be forcibly varied over ranges of

± 20 per cent, with no significant overshoot or undershoot.

Wet bulb temperature is measured by the wet-bulb thermometer seen at WBT (Fig. 3), the bulb of which lies in the de-

scending air stream from the circulating blower in the roof, and is protected by baffles from the added wet, dry or cool air coming from beneath the floor baffle. WR (Fig. 3) is a water reservoir for this

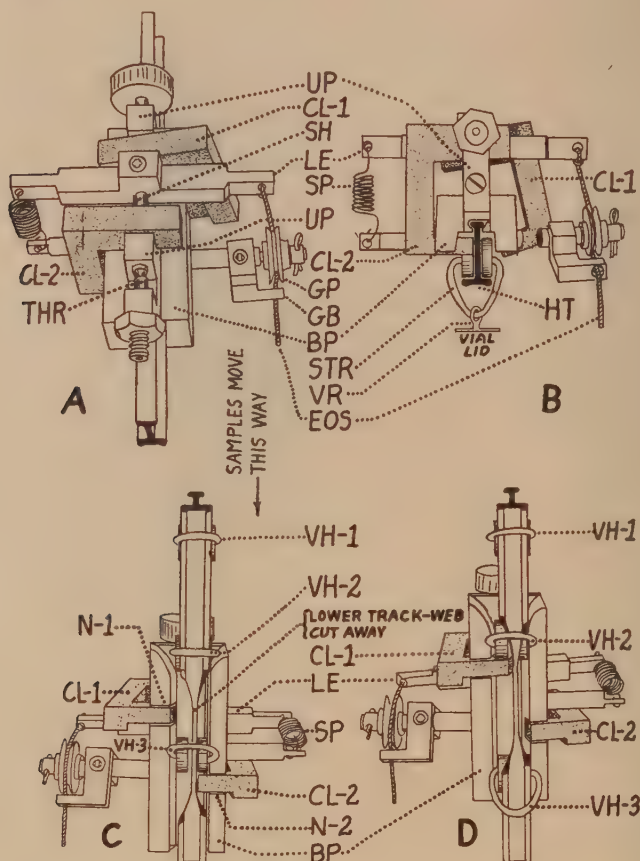


FIG. 13. Sundry views of the escapement. 13A, looking up-track and downward, 13B, looking straight up-track, 13C, looking upward from underneath, escapement "closed," 13D, similar to previous view, but escapement "open." Note how, in Figure 13D, the vial hanger (VH-3) has passed beyond Claw No. 2 (CL-2), moving towards the tunnel, having been released by the outward swing of Claw No. 2 as the operating string opens the escapement. BP, basal part, which holds all the rest, and clamps to the track, being split into right and left halves; CL-1, up-track claw, retracted when the escapement is "closed"; CL-2, down-track claw, rests against track web when escapement is closed, and holds back samples; EOS, escapement operating string, when pulled, opens escapement; GB, guide block for EOS; GP, smooth-running pulley for EOS; HT, helical track; LE, escapement lever, when pulled down by EOS, opens escapement; N-1, notch for CL-1; N-2, notch for CL-2; SP, escapement lever spring, holds escapement "closed"; STR, U-shaped stirrup of standard "Harrison" hanger; THR, thrust-pin to take downward thrust of weight of samples; UP, upper part of escapement; VH-1, VH-2, VH-3, successive vial hangers; VR, small ring fastened to lid of vial. The hanger threads through it to suspend the vial.

bulb. The structure SC of Figure 3 is a set of spare binding posts for 6-volt current.

Helical track mechanism in the warm chamber. Referring to Figures 3 and 19, this track in each of WC and SC consists of three turns of "Harrison" brass curtain-rail, the turns being 15 in. in diameter with a downward slop of approximately 10 degrees. This helix HT is supported by a center rod HCR by means of radial supporting arms RSA, tipped with standard "Harrison" rail-holders. The whole helix is thus easily adjustable for slope etc., when first installed. The helix continues by a short straight portion and, in Figure 3, disappears into the tunnel at the lower left appearing again in Figure 19 at the upper right. This straight part of the track carries the escapement (E, Figs. 3, 13) which holds back the train of vials hanging on the track. The string EOS is the escapement-operating string, discussed below, which passes from one of the doors in the tunnel, and works the escapement as the door opens. ELS is a spring to give some elasticity in the escapement-operating mechanism. The escapement is described below.

Samples and their suspension on the track. At present, the replicated cultures, or samples, are housed in plastic vials (Figs. 1, 3, 19) 3 in. high and $1\frac{3}{4}$ in. diameter (The Celloplastic Corporation, Newark, N. J.) with screw caps. It is intended later to design an aluminum rack to hold several vials, thus running several species through at once. Six holes $\frac{3}{8}$ in. in diameter are punched in the cap for ventilation, and are covered with 76-mesh silk bolting cloth. To the top of the cap is soldered a little ring (VR, Fig. 13) through which the U-shaped stirrup of a standard "Harrison" roller-fitting is threaded. Thus the sample vials on the track like monorail cars. Incidentally, to obtain smooth and certain rolling when the escapement opens, and to avoid sticking in the escapement, it was necessary to reface the periphery and the two flat faces

of every roller (there are two per hanger) to the nearest 0.001 in., gauging each one, and also setting the gap of the stirrup to just the right spacing. Bronze rollers work better than aluminum, which is soft and easily dented.

It was found that all was well, the escapement working perfectly, when there were only say, 10 samples on the track. When there were say 50, the component of the weight pushing down the track, tended to squeeze some vials out so that instead of hanging vertically, they hung at a pronounced outward slope. This jammed the escapement and spilled flour. To prevent this, each vial is equipped with a rubber "anti-squeeze" ring fitted just below the lid as seen at SRR in Figures 3 and 19. This ring is $\frac{1}{2}$ inch wide by $\frac{1}{8}$ inch thick and is made by stapling-up a suitable strip of sponge rubber. It effectively prevents squeezing and cushions the whole assembly. Incidentally, the rings do *not* work if placed around the base of the vials.

The escapement. This part of the apparatus gave more trouble in design than any other, a total of eight models being made and discarded before success was attained.

The present model, Figure 13, consists of a base portion BP, split into two halves. It clamps around the upper flange of the track by two screws (not shown). This basic part is projected upward in line with the track flange as a part UP, which is milled out to take the shaft SH, carrying the escapement claws, CL-1 and CL-2, held to the shaft by socket set-screws. THR is a hardened steel pin with an end dimple which bears against a 60° hardened steel point on the end of the shaft SH, and carries the end-thrust from the weight of the samples. This pin can be so set that the claws move freely in the notches N-1 and N-2, cut in BP (Fig. 13C).

The shaft SH also carries the lever LE which, when pulled down at one end by the string EOS, rotates the shaft through a small angle, causing claw CL-2 to move

away from the web of the track at its tip, while claw CL-1 moves towards it. GP (Fig. 13A) is a guide pulley for EOS, while GB is a guide block to keep the string lined up with the groove in the pulley. The lever LE is returned by the spring SP, when the doors begin to close, and tension on the string is relaxed.

The action is as follows. In the resting state, the spring SP keeps the lever LE tilted back, and the claw CL-1 is away from the track-web as in Figures 13A, 13B and 13C. Thus the way is open into the escapement, and the whole train of vials is held back by CL-2 which bears against the track-web. The second vial up the train is outside the escapement, while the first, bearing against CL-2, lies between CL-1 and CL-2 inside the escapement. When the string is pulled, the tip of CL-1 approaches the track and blocks off the train of vials. A little later, CL-2 moves out far enough to release the first vial as in Figure 13D, and this vial runs away through the tunnel. When the string relaxes again, CL-2 moves inward, blocking the track, while CL-1 moves outward until the train of vials is released, and moves down one place, coming to bear against CL-2 which by this time has come to touch the track-web. Thus if the lever, LE, be "jiggled" up and down, the train of vials will flow through the escapement, one vial at a time, one for each down-and-up movement of the lever.

Parenthetically, the difficulty in design of such an escapement arises from the fact that it must work with a small pull, though holding back a quite large force. It must have absolutely no "servo-action" tending to lock it or unlock it under the push of the vials. Thus it has to be very massive, and the faces of the claws must be accurately at right-angles to the track-web.

The program controller. In order to make clear the operation of the tunnel (leading to the cool storage chamber) it is necessary to interpose here a description of the program controller.

All program controllers depend for their

action upon feeding through their mechanism some form of notched cam, punched strip or some other kind of specially deformed body, whose deformations, passing through the mechanism at appropriate times, cause it to function.

All types of cams or punched strips are difficult and often expensive to make, and are not easy to change when once made. For long programs of perhaps several thousand hours, the perforations or notches must be impracticably small if the cam or tape is to be of manageable size.

After numerous trials, faced with the above difficulties, the controller was designed so as to use a linear series of bronze balls which, when fed through it, act like a succession of coins in a coin-operated vending machine. Two sizes of balls are used, $\frac{3}{16}$ in. and $\frac{1}{4}$ in. When a small ball is fed in, it drops right through, and no action results. When a large ball is fed in, it sets the sampling mechanism in operation, and a sample is drawn. If the series of large and small balls be so arranged that, one ball being fed in each hour, a large ball arrives at each sampling-hour, and a small ball at all other hours, any program of sampling can be effected. This method is derived from an apparatus devised by the writer some years ago (Stanley 1939) to administer impact stimuli to experimental animals by dropping steel balls on them. In the present apparatus, bronze balls are used because steel balls become magnetized, and will not feed properly.

The series of balls forms an infinitely adjustable linear "cam," which can be changed in a moment by interchange of ball-sizes. It costs nothing to set up, and the balls for a future portion of the program are simply stored in racks, and loaded into the magazine as required and in the order as determined from a program-diagram previously decided upon. A series of balls which produces sampling every other hour shows in the long trough-like magazine in Figure 15, which is a slanting downward view of the rear of

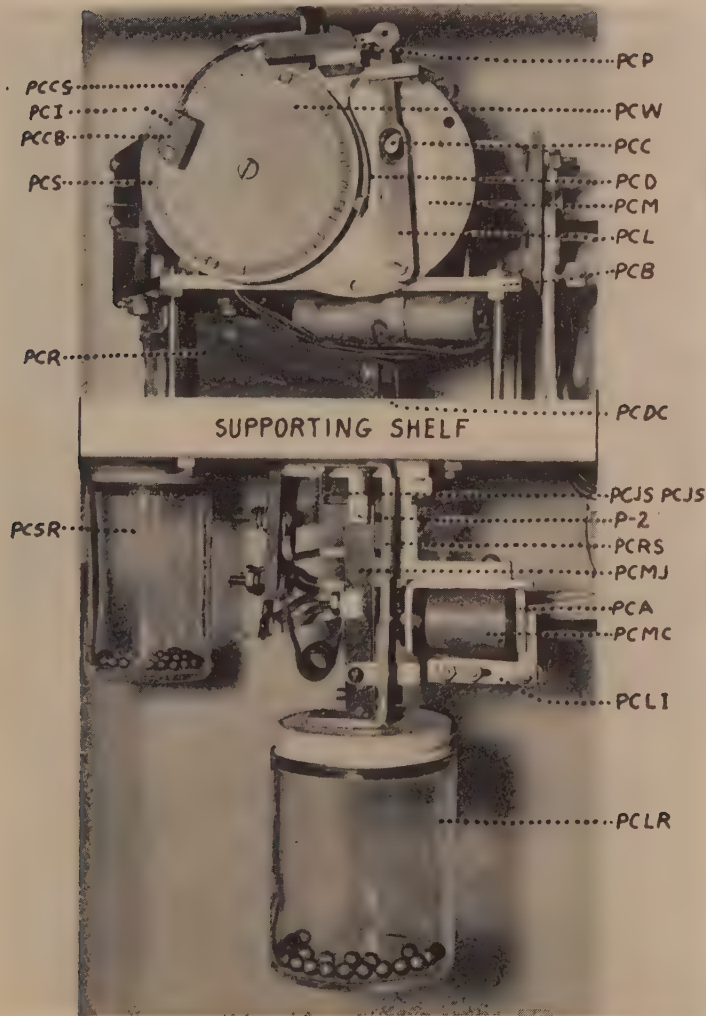


FIG. 14. Front view of program controller. NOTE: the controller stands on a shelf, with the beak-switch below the shelf. The white stripe across the figure is the turned-up flange of the angle-iron edge of this shelf. PCA, armature of beak-switch opening-magnet; PCB, controller base; PCC, controller cam, driving oscillating arm for time-wheel; PCCB, contact block for hammer circuit, which flips balls from magazine; PCCS, contact springs of hammer circuit; PCD, detent spring for time-wheel; PCDC, delivery chute for large balls, to beak-switch; PCI, insulating block for PCCB; PCJS, beak-switch jaw spring, holds switch "closed"; PCL, oscillating lever driving time-wheel pawl; PCLJ, linkage from beak-switch opening-magnet to moveable arm of this switch; PCLR, large-ball reservoir; PCM, drive motor of controller; PCMC, opening-magnet of beak-switch; PCMJ, moveable jaw of beak-switch; PCP, actuating pawl transferring motion of oscillating arm to time-wheel; PCR, sieve rails transporting large ball to beak-switch; PCRS, support of large-ball reservoir; PCSR, small-ball reservoir; PCS, time scale on time-wheel; PCW, time-wheel; P-2, pivot of moveable jaw of beak-switch.

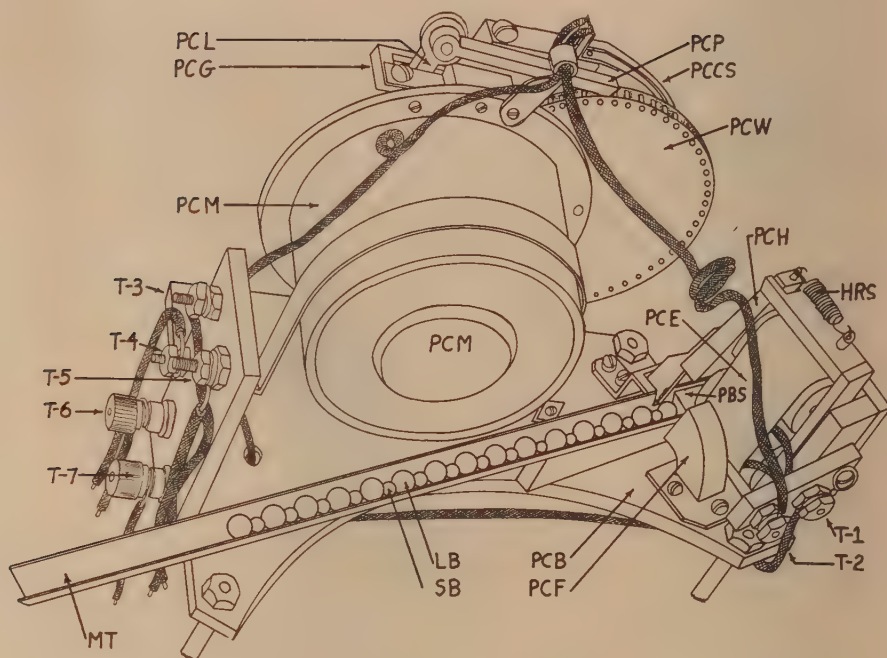


FIG. 15. View of program controller from above and behind. HRS, hammer return-spring; LB, large ball; MT, magazine trough for balls; PBS, ball stop; PCCS, contact springs which, when shorted, cause ball to be flipped out; PCB, base part; PCE, electro-magnet operating hammer to flip balls; PCF, delivery funnel for balls going to sieve rails; PCG, guide for pawl-operating lever; PCH, hammer which flips balls; PCL, lever which oscillates and works pawl; PCM, main driving motor of controller; PCP, pawl, driven by PCP, turning time-wheel; PCW, time-wheel; SB, small ball; T-1, 6-volts, positive, from terminal board to PCE; T-2, 6-volts, negative, from PCCS; T-3, 6-volts, negative, from terminal board to PCCS; T-4, 6-volts, negative pick-up to supply beak-switch, being bridged behind to T-3; T-5, 6-volt positive input, connects to T-1; T-6 and T-7, 110-volt A.C. for PCM.

the controller (shown also in front view in Figure 14).

Referring to figures 14 and 15; on the base PCB is mounted a General Electric Synchronous Inductor Motor (Model 5SMY-50J) shown as PCM in the figures. It rotates a cam, PCC, at 1 r.p.m. and this causes the lever-arm PCL to oscillate left and right with each revolution, about the pivot P-1 seen at its lower end. This causes the pawl PCP to move to and fro on the periphery of the time wheel PCW. This wheel has 60 "teeth" in its edge, made of $\frac{1}{32}$ in. piano-wire pins bridging a groove in the periphery (the time wheel is really a gigantic "lantern gear" of the sort found in

clocks). Referring to Figure 14, when PCL moves to the right, the pawl rides back over a tooth, and when it moves to the left, it pushes this tooth to the left and rotates the time wheel $\frac{1}{60}$ of a revolution. These discontinuous movements of the time-wheel are made sharp and abrupt by the detent-spring PCD, which carries a hardened steel wedge at its tip. This wedge rides over the tooth pins and locks the wheel between jumps by falling between two teeth. Thus, in operation, the wheel moves "protestingly" at first, as the detent wedge mounts a tooth, and then "jumps" to the next space as the wedge rides over the tooth into the next inter-tooth space.

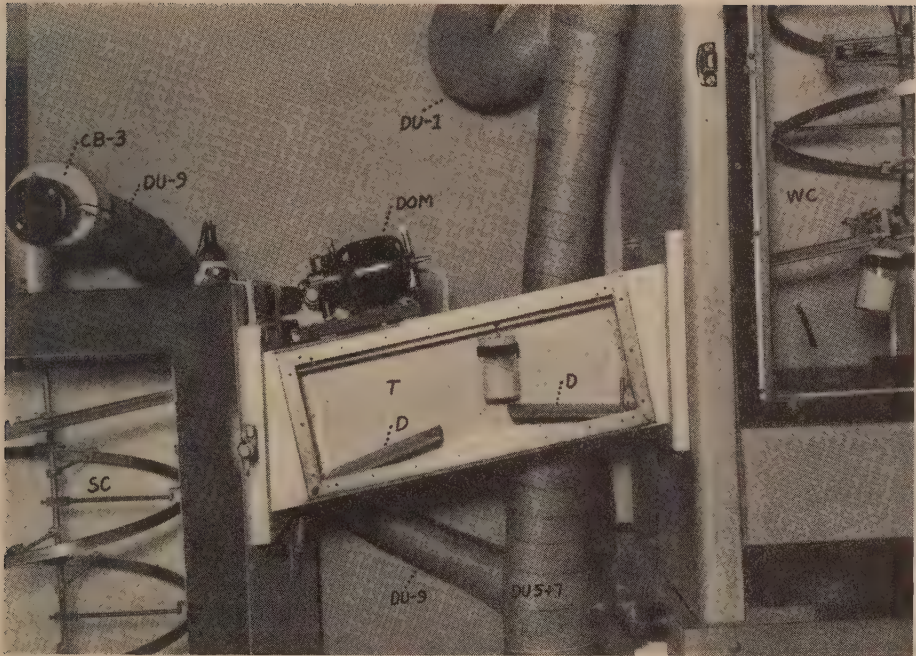


FIG. 16. Front view of tunnel connecting warm chamber to cool storage chamber. CB-3, blower forcing cold air from main cooling chamber to cool storage chamber; D, tunnel doors; DOM, door-opening motor; DU-1, air duct carrying warm air to heat-exchanger labyrinth; DU-5 + 7, air ducts carrying air to be humidified (DU-5) and to be dried (DU-7), from the warm chamber to the humidifier and de-humidifier; DU-9, air duct carrying air from main cooling chamber to CB-3; SC, cool storage chamber; T, tunnel joining warm chamber to cool storage chamber; WC, warm chamber.

The time wheel has a scale of minutes around its face, as shown at PCS, Figure 14. Opposite the zero-minute is an insulating block PCI, bearing an embedded copper block PCCB, insulated from the time-wheel. As this time-wheel rotates, this copper block finally comes to pass (at the zero-minute) under the tips of the two contact springs PCCS. It shorts them, thus actuating the electro-magnet PCE and pulling the hammer PCH forward. This flips the lowest ball of those in the magazine into the collecting funnel PCF.

The flipped ball falls through the funnel and arrives at the upper end of the two brass sieve-rails (PCR, Fig. 14). These are spaced $\frac{7}{32}$ in. apart, and a small ball will fall through them into the

small-ball reservoir PCSR. A large ball cannot pass the sieve-rails, and rolls down between them, to decant into the delivery chute, PCDC, leading to a special switch, the so-called "beak-switch," which occupies much of the lower part of Figure 14.

This beak-switch consists of two jaws: a fixed jaw of brass, concealed behind PCRS (the support of the large-ball reservoir in Figure 14) and a moveable jaw PCMJ, made of bakelite and faced with brass. This jaw pivots around the point P-2. The assembly is thus similar to a bird's beak, with PCMJ acting as the lower jaw or mandible. The spring PCJS mimics the masseter muscle, acting to close the beak.

In the resting condition, the beak is "closed" and if a large ball comes down

the delivery chute it sticks in the beak as if it were a large seed regurgitated by a bird, and too large to pass out of the bird's beak. This ball completes the circuit between the fixed and moveable jaws and thus closes a relay (D-1, Fig. 20) supplying 110-volt A.C. current to the door motor (DOM, Figs. 16, 17, 18). If this ball stayed indefinitely in the beak-switch, it would keep this relay closed and the doors would swing open and shut endlessly. It is therefore necessary to drop the ball out of the beak-switch at some time during the first open-and-shut motion of the doors. This is done by the

cam-switch (DCS, Figs. 17, 18) which, when the doors are wide open, completes a circuit through the magnet coil PCMC (Fig. 14). The armature PCA (Fig. 14) then pushes the beak open through the linkage PCLI, and the ball drops into the large-ball reservoir PCLR. Later in the door-motion cycle, the "beak-switch" is closed again by the same cam-switch. The details of this switching are discussed in connection with the tunnel and door mechanisms.

Returning now to the time-wheel. This is quite free on its shaft, and can be turned against the resistance of the de-

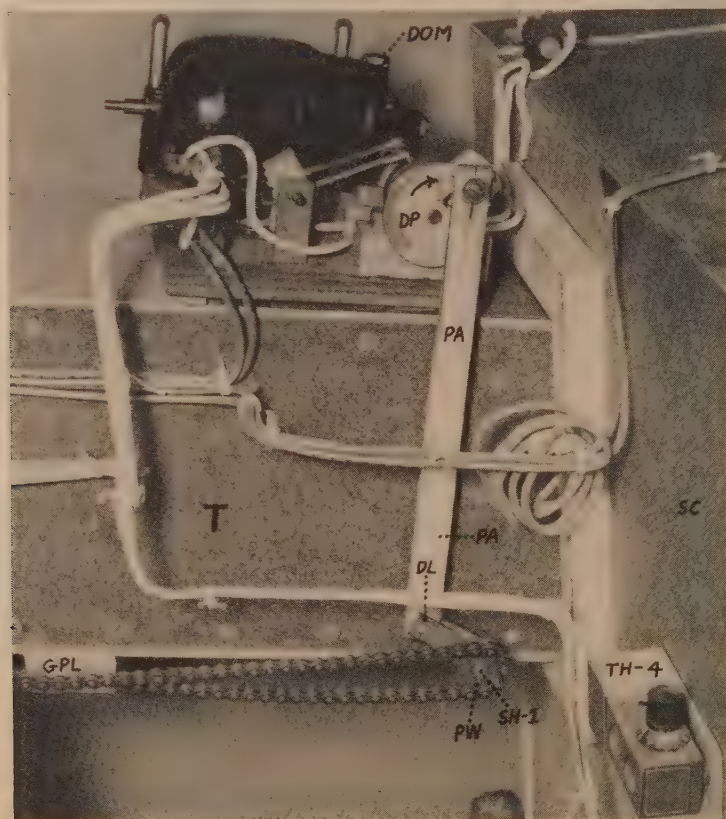


FIG. 17. Rear view of door-opening mechanism and tunnel. DOM, door-opening motor; DP, drive plate of door-opening mechanism; DL, drive lever; GPL, guide plate of chain; PA, pitman arm connecting drive plate to door sprocket; PW, primary door sprocket (there is a second sprocket on the other door shaft); SC, cool storage chamber; SH-1, door shaft, acts as a hinge for door; T, tunnel; TH-4, thermostat controlling temperature of cool storage chamber.

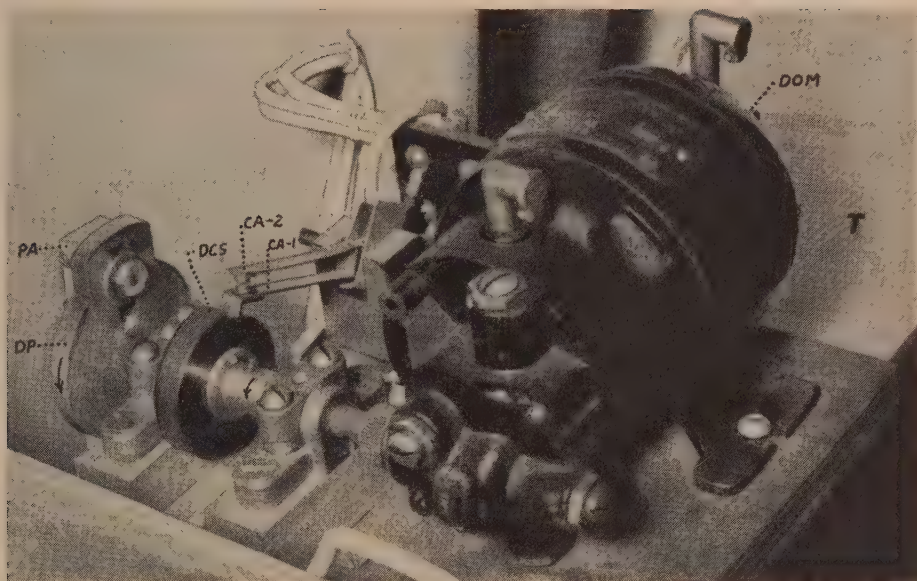


FIG. 18. Door-opening motor and rotary switch. CA-1, CA-2, contact arms of rotary switch; DCS, cam actuating rotary switch; DP, drive plate of door-opening mechanisms; PA, pitman arm of mechanism; T, tunnel.

tent PCD so as to bring it into synchronism with the clock time, *i.e.*, one brings the proper minute on the scale under the tips of the springs PCCS. In Figure 14, the time is 3 minutes past the hour. The total of elapsed hours is shown on a magnetic counter operated by the same pulses which work the ball-hammer PCH. This counter is not shown in the figures. When sampling is complete, the wheel moves onward $\frac{1}{60}$ revolution, the ball-hammer flies back, the balls all roll down one place in the magazine, and the controller lies in wait for the next hour. (See Table I for timing of the door-cycle.)

The tunnel and its mechanism. The tunnel, shown in Figures 16 and 17 is built around an accurately-made frame of 1 in. by $\frac{1}{8}$ in. brass angles milled exactly to shape at the corners and brazed together. This frame is then covered with tempered Masonite, held on by machine screws. At the front is a plexiglass window. The brass monorail track contin-

ues through just under the roof of the tunnel, and in Figure 16 a sample is shown half-way through the tunnel, with the doors open. The doors are notched at their upper edges to seal fairly well around the track when closed. The doors, D, Figure 16, are made of two $\frac{1}{4}$ -in. slabs of tempered Masonite with aluminum foil between, and are fastened by a brass sleeve along the hinge-edge to steel shafts which pivot in holes drilled in the brass tunnel frame. The shafts are $\frac{5}{16}$ in. drill-rod.

In Figure 17, which shows the rear of the tunnel, it will be seen that door-shaft SH-1 carries a sprocket-wheel PW, meshing with a $\frac{3}{16}$ -in.-pitch roller chain which passes over a similar sprocket on the shaft of the other door. The chain is crossed at the guide plate GPL. Thus, if one door be opened, the other also opens, and *vice versa*. On SH-1 is a lever-arm DL, connected by a pin to the pitman arm PA, which in turn connects to the drive-plate DP on the door-motor

shaft. When the motor is made to run by a ball dropping into the beak-switch and closing D-1 relay, the door motor DOM (Figs. 16, 17, 18) rotates the door-motor shaft through 1 revolution in the direction of the arrow on DP. Through the linkage of PA and DL, this opens the doors and closes them again.

Control and timing of this single revolution are effected as follows. When the ball drops into the beak-switch, and power is supplied to the door-motor through D-1 relay, this power comes direct to the door-motor, and the doors begin to open. This rotates the door-motor shaft and with it, the cam DCS of the door cam-switch. In Figure 18, the cam is shown as it is when the doors are closed, with the contact arm CA-1 resting on a low part of the cam, and thus not contacting the arm CA-2. As the cam rotates, a portion of greater radius will arrive under CA-1 and lift it into contact with CA-2. This occurs just before the doors are fully open. This contact closes the circuit through the coil PCMC (Fig. 14) and opens the beak-switch, dropping the ball out of the beak-switch. At the same time, the same circuit closes a relay D-2 (Fig. 20) to provide an alternate power supply to the door-motor (D-1 having opened due to the loss of the ball from the beak-switch).

The doors move to fully open, operate the escapement, slip the sample, and without pause, begin to close again. Just before they are closed, CA-1 slips off the declivity of the high part of the cam DCS, onto the low part as shown in Figure 18, and power to the door motor is interrupted since this opens D-2, and D-1 is, as explained, already open. The door-motor and door assembly then coast to a stop with the doors firmly pressed against the sponge-rubber seals around their frames. The position of the cam DCS, of the doors relative to their sprockets, of the radius of the drive-plate DP, of the position of the lever DL in relation to the doors, etc., etc., are all adjustable, and when properly adjusted relative to

each other, the drive is silent, smooth and exact.

The door-motor is a Bodine Electric, Type CAR-2, 1,500 r.p.m., geared down to turn the final shaft driving the doors at 1 revolution in 42 seconds (reduction 1,050 : 1), against load. The actual time-sequence of sampling is as shown in Table I.

The cool storage chamber. This is a chamber (see Fig. 19) with inside dimensions: 20 in. wide, 22 in. deep and 30 in. high with a three-inch wall consisting of

TABLE I. *Timing of events in sampling*

Time, seconds	Event
0.00	Ball drops, enters beak-switch, D-1 relay closes, doors begin to open
17.00	CA-1 contacts CA-2, beak-switch opens, ball drops out, D-1 opens, D-2 closes, door-motor continues on power through D-2
18.00	Doors nearly open, escapement opens, sample begins to run
18.25	Sample through tunnel
21.00	Doors fully open, reverse and begin to close
27.00	Escapement closes, samples move down one place, ready for next sampling operation
42.00	CA-1 slips off declivity of cam, D-2 opens, power to door-motor cut off, beak-switch closes
60.00	Contact broken on hammer circuit, hammer flies back, balls in magazine move down one place, ready for next sampling operation

the following layers from outside in: Masonite, aluminum foil, "Ten-Test," aluminum foil, "Ten-Test," aluminum foil, Masonite, aluminum paint. The door is sealed by a heavy sponge-rubber gasket and screw clamps.

This chamber is controlled for cooling only. The DeKhotinsky thermostat (TH-4, Figs. 17, 19) controls a blower (CB-3, Fig. 8) which blows cold air as required from the main cooling chamber via duct DU-9 (Fig. 8). This air enters through the roof, above a baffle RB (Fig. 19), spreads through the chamber, and leaves under the floor baffle FB-2 returning to the main cooling chamber via a duct which cannot be seen in any figure, being tucked underneath the

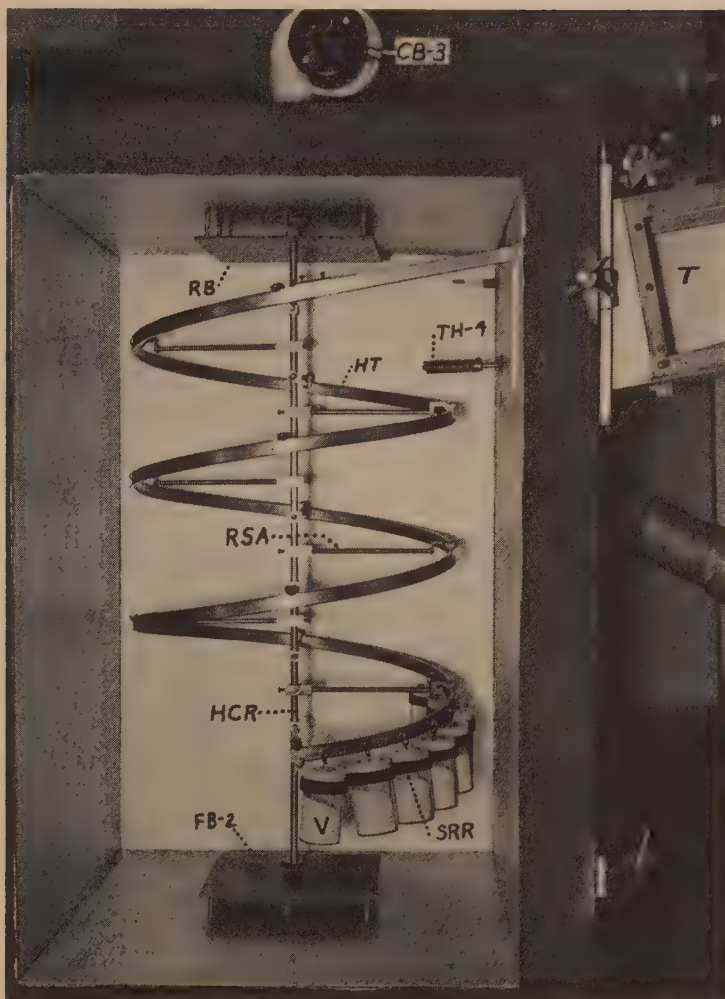


FIG. 19. Front view inside the cool storage chamber. FB-2, floor baffle; HCR, center support rod for helix; HT, helical track; RB, roof baffle; RSA, radial supporting arm of helix; SRR, soft rubber anti-squeeze ring; TH-4, thermostat controlling cooling; V, sample vial.

chamber. This air flow affects the thermostat directly, thus cutting off overshoot. Control is effective to about 0.25°C ., with some small variation throughout the chamber, but as it is necessary only to keep well below the minimum effective temperature, these variations are negligible. The chamber can, if need be, be lowered to 0°C ., but is usually kept at about 8°C .

The chamber contains the storage helix,

identical with that in the warm chamber, except that it has no escapement, but merely a stop at the bottom.

The main cooling chamber. This is a large chamber (Figs. 1, 8) 22 in. wide by 33 in. deep by 42 in. high inside, with walls similar to those of the cool storage chamber, except for a heavy galvanized iron lining. The chamber is cooled by a large finned expansion coil supplied by a two-cylinder Frigidaire compressor

(Model 16K3287-AF250) (CO, Fig. 8), driven by a $\frac{1}{2}$ -horsepower motor and using Freon as a refrigerant. This machine is ample to supply the autotrephon and also four small cooled chambers shown in Figure 2, but it would be a little hard-pressed in hot summer weather. Prospective builders of an autotrephon would do well to use the next largest size.

Ducting. The air ducts are flexible spirally wound tubing, with cotton-packed joints, $1\frac{1}{2}$ in. inside diameter, made of galvanized steel. This rusts in time, and

it is intended to replace these ducts by $1\frac{3}{4}$ in. stainless steel tubing. They are insulated with the following layers from outside inward: water-proof building paper, $1\frac{1}{2}$ inches of hairfelt, aluminum foil. This seems reasonably adequate, but even more insulation would cut the load on the compressor.

Time lag in cooling of samples. The success of the autotrephon depends upon the samples being cooled below the minimum effective temperature quite rapidly, on transfer to the cold storage chamber.

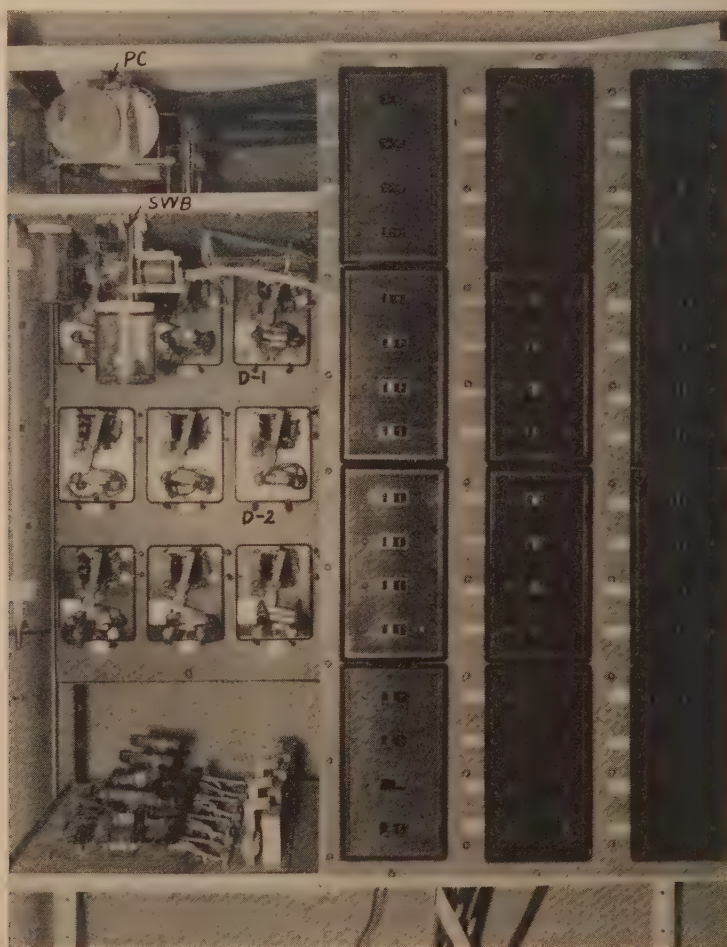


FIG. 20. Front view of control console. D-1, primary door-motor relay; D-2, secondary door-motor relay; PC, program controller; SWB, beak-switch.

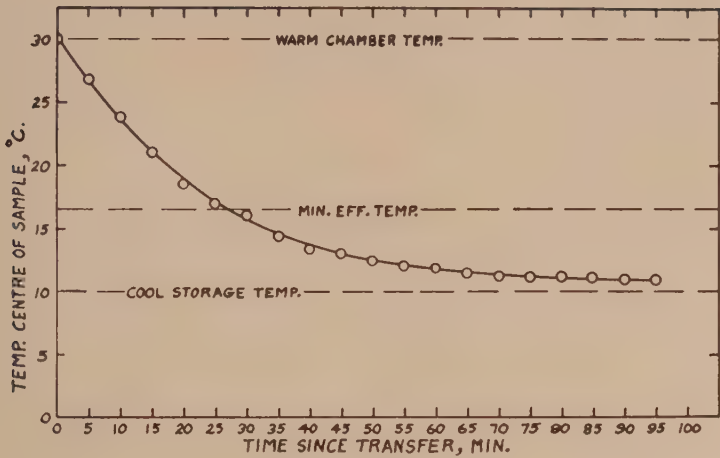


FIG. 21. Rate of cooling of a sample vial when transferred to the cool chamber. Warm chamber: 30° C.; cool storage: 10° C.; vial: standard plastic as described above; medium; whole wheat flour through 50-mesh, relative humidity about 50%; weight of medium 30 gm.; depth of flour in vial of diameter 1.68 in. is 1.3 in.; thermocouple: 28-gauge copper-constantan without any covering.

This question has been examined by means of a thermocouple inserted in a typical sample vial. For a vial containing 30 gm. of whole wheat flour, packed as is customary in this laboratory (by shaking the flour to level it, and bumping the vial firmly once on a slate slab covered with thick paper), and with the thermocouple in the geometric centre of the flour mass, with the warm chamber at 30° C., and the cool storage at 10° C., the rate of cooling is as shown in Table II and Figure 21. It will be noted that the minimum effective temperature for *Tribolium confusum*

(about 16.5° C.) is reached in 26 minutes. This is negligible in terms of the variability of the material, but it can be shortened to as little as 15 minutes by reducing the temperature of the cool storage still lower. If one wishes to be very exact, a correction factor could be worked out for the slight amount of growth which would occur in this interval, but it hardly seems worth while. Table II is based on dry whole wheat flour, which is a poor conductor of heat. Many other foods would cool more rapidly.

TABLE II. Rate of cooling of a sample transferred from 30° C. to 10° C., in the autotrephon

Time since transfer, minutes	Sample temp. ° C.	Time since transfer, minutes	Sample temp. ° C.
0	30.00	50	12.40
5	26.80	55	12.00
10	23.80	60	11.80
15	21.00	65	11.40
20	18.60	70	11.20
25	17.00	75	11.10
30	15.80	80	10.90
35	14.40	85	10.80
40	13.40	90	10.70
45	13.00	95	10.65

PROGRAM PLANNING FOR THE AUTOTREPHON

The autotrephon as described above has been in active use since January 1, 1950, and a number of different programs have been used. Programs can be varied not only as to the time of sampling, but also by what may be called "tracking," a general term to describe the ways in which the vials are loaded, interspersed or linked on the track, thinking also of the way in which the ball-magazine is loaded. Some programs follow which may be of interest to other workers.

TABLE III. *Typical program diagram for single-species, single, non-linked tracking, with sampling every 5 hours*

Time, hrs.	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	etc.
Vial loading						A					A					A			
Ball loading	o	o	o	o	o	O	o	o	o	o	O	o	o	o	o	O	o	o	etc.
Sample taken						#					#					#			etc.

Single tracking, non-linked

This means that the vials are loaded into the helix in one linear series, and are not connected together in groups as described under "linked" tracking. All the description of the apparatus so far in this paper has been on the tacit assumption of this sort of tracking.

Single, non-linked tracking is used for the study of one species at a time, with sampling at any intervals, as shown by the program of Table III. It can also be

intervals in each series may be varied within limits.

Multiple species, linked tracking

When using this method, a small wire stirrup (we make them from a paper clip) is pushed into the rubber anti-squeeze ring of adjacent vials, so as to tie them together into trains of two or more vials. The ball-loading in the magazine is then arranged as explained below, so that these trains move to the cool chamber as units.

TABLE IV. *Typical program diagram for multiple-species, single, non-linked tracking. Three species, sampling every three hours for each species*

Time, hrs.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	etc.
Vial loading			A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	etc.
Ball loading	o	o	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	etc.
Sample taken			#	#	#	#	#	#	#	#	#	#	#	#	#	#	#	etc.

used to study more than one species at a time by interspersing the vials of the various species, as the helix is loaded. Typical programs are shown in Tables IV and V, but it should be noted that if N species are used, any one of them cannot be sampled more often than once every N hours unless a sample of another species is sacrificed. Furthermore, this method gives individual sampling of each species, and the observations on each species form a separate time series, though the intersample

Thus the apparatus samples trains rather than single vials. Referring to Table VI, suppose there are three vials in each train, and that a train is to run out to the cool chamber at 10 P.M. A large ball is allotted in the magazine for 8, 9 and 10 P.M. The 8-P.M. ball releases the first vial of the train, but this vial does not run away because of its linkage to the second vial. Similarly at 9 P.M., another vial gets through the escapement, but cannot run further, and at 10 P.M. the last vial gets

TABLE V. *Typical program diagram for multiple-species, single, non-linked tracking. Three species, sampling of each species individually, every 5 hours*

Time, hrs.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	etc.
Vial loading					A	B	C			A	B	C			A	B	C	etc.
Ball loading	o	o	o	o	O	O	O	o	o	O	O	O	o	o	O	O	O	etc.
Sample taken					#	#	#			#	#	#			#	#	#	etc.

through and the whole three run together to the cool chamber.

With such a program, and N vials in a train, sampling of a given species cannot be more often than once in N hours and there are also many fruitless openings of the tunnel doors, though this is of no real importance, apart from wear and tear. The advantage is that sampling of all N species is contemporaneous.

These are push-button operated, and can be worked to pass one or more vials to the lowest turn of the helix as required. These had not been installed when the figures for this paper were made, and thus do not show in any figure.

Mixed tracking

In some cases, where linked tracking is used, it may be necessary on some oc-

TABLE VI. Typical program diagram of multiple-species, single, linked tracking, simultaneous sampling of three species every 5 hours

Time, hrs.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	etc.
Vial loading*			A—B—C					A—B—C					A—B—C					etc.
Ball loading	o	o	O	O	O	o	o	O	O	O	o	o	O	O	O	o	o	etc.
Sample taken					#					#					#			etc.

* The dashes in A—B—C indicate wire links.

Multiple species, "racked" tracking

With this method, the vials are placed in small racks holding two or more vials, and these racks are hung on the roller hangers of the helix. A large ball then releases a whole rack, and so N species can be sampled every hour if need be.

casion to sample at a shorter interval than the method will allow (i.e., at less than N hours, with N species). In such a case, "racked" tracking may be used in this region of the program, as shown in Table VII. It will be obvious to the reader that, with some care and thought, combined with ingenious loading of the balls, almost

TABLE VII. Typical program diagram of multiple-species, multiple (or racked) tracking, non-linked, giving simultaneous sampling of 3 species every 7 hours

Time, hrs.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	etc.
Vial loading							A B C							A B C						
Ball loading	o	o	o	o	o	o	O	o	o	o	o	o	o	O	o	o	o	o	o	etc.
Sample taken							#							#						

There are some obvious limitations in the matter of the size of the racks, and the down-track thrust on the escapement must be borne in mind. If this is too great, the escapement may jam. For the McGill Autotrephon, the track loading bearing directly on the escapement should not exceed about 30 vials, each with 30 gm. of flour. The remainder of the loading of the helix is held back by solenoid-operated helix stops, located one at each turn.

any conceivable program can be carried out with any reasonable number of species (see Table VIII), all at the same time, though of course, all must be exposed to the same conditions of temperature and relative humidity in the warm chamber, during the program.

Special escapements

The escapement described in this paper, and shown in Figure 13, passes one vial

TABLE VIII. *Typical complex program diagram of multiple-species loading, with mixed types of tracking, and individual and simultaneous sampling. This is an unlikely plan, but it shows what can be done. Note how multiple tracking around 8, 9 hours permits close spacing of samples*

Time, hrs.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	etc.
Vial loading			A—B—C	D				A B C	A D	A	B	C	D			A—B		C—D		
Ball loading	o	o	o	o	O	O	o	O	O	O	O	O	O	o	o	O	O	O	O	O
Sample taken					#	#		#	#	#	#	#	#				#		#	
Species sampled					A B C	D		A B C	A D	A	B	C	D				A B		C D	

(or rack of vials) at each drop of a large ball. Cases may occur in which it is desired to run a very large group, say 25 to 30 vials through the tunnel at one time (whatever that time may be). In such a case, Claw No. 1 (Fig. 13) is backed away from the track-web by loosening its set-screw and re-tightening in the backed-off position. Now when the escapement-operating string pulls as the doors open, Claw No. 2 recedes from the track web in the usual way, but Claw No. 1 is too far out to reach the web as it comes forward, and so does not hold back the remainder of the series of vials, and the whole series scoots through the tunnel. A clamp on the helix will hold back any that are not to go, and these can be lowered down to the helix for the next exodus.

Consideration is being given to the design of a special switch, operated by the door-motion. This will be quickly adjustable to give 1, 2, 3 or more pulses which will in turn, via a solenoid, open the escapement 1, 2, 3 or more times, thus passing more than one sample-vial for one large-ball drop. This could take the place of linked or rack tracking, but unless the same number of vials is to run out at each sample-hour, the pulse-switch will have to be altered by a visit to the laboratory, and this in a way defeats the whole philosophy of the autotrephon.

Work with alternating temperatures, using "replacement" tracking

It is sometimes desirable to have specimens exposed successively to two alternat-

ing temperatures. This can be done on the autotrephon by setting the two chambers (cool and warm) appropriately, and running groups of vials from the warm to the cool, after retracting Claw No. 1, as above. The vials must then be replaced on the warm-chamber helix by hand, but this can probably be done during business hours. If this is not possible, there is nothing to stop someone building a "cascade" type of autotrephon, with several successive chambers, tunnels, etc., but the writer would prefer not to be there when such a monstrosity is under construction.

The checking system

It has been pointed out to the writer that one cannot be sure, with intricate tracking procedures, that samples actually have been transferred as intended. To offset this difficulty, which could be quite troublesome, a checking system has been added to the apparatus subsequent to the preparation of the main manuscript. It was intended originally to design a purely mechanical system, free from the possibility of electrical troubles, but this did not prove to be feasible. The electrical system described below operates from the main 6-volt D.C. battery, and seems very reliable.

A temperature and relative humidity recorder giving wet and dry bulb temperatures has been installed (it sits on top of the control console of Fig. 20). Two additional pens have been added to it, and write on its drum. One pen has its operating magnet connected to the terminals

Technician and Instrument Maker for the Department of Zoology at McGill University, who constructed the whole of the apparatus except the program controller, the escapement and the wiring. Mr. Pollock took a most enthusiastic interest in the whole project, and it could not possibly have been carried to completion without him. Design proceeded largely by conferences and trial and error, and it is due to Mr. Pollock that this method worked as it did. It is thus a pleasure to acknowledge the help of one who is both colleague and friend.

The writer is also indebted to McGill University, who paid the bills, including excess publication costs, and to Miss Helen J. Martin who looked after the apparatus and examined the samples when other duties became too strenuous to allow the writer to function.

LITERATURE CITED

- Stanley, J. 1939. A device for administering impact stimuli to experimental animals. *Journ. Comp. Psychology*, **28**: 93-96.
- . 1946. The environmental index, a new parameter as applied to *Tribolium*. *Ecology*, **27**: 303-314.

THE RETURN OF NATIVE PERENNIAL BUNCHGRASS
FOLLOWING THE REMOVAL OF KLAMATH
WEED (*HYPERICUM PERFORATUM* L.)
BY IMPORTED BEETLES¹

CARL B. HUFFAKER

Division of Biological Control, University of California, Albany, California

INTRODUCTION

During the relatively short period of 4 years since release of imported beetles which feed on it, Klamath weed, *Hypericum perforatum*, a serious weed on perhaps a million or more acres of Western range lands, has been brought under strikingly successful control in limited areas by this tool of applied ecology. Though the range in question has not yet been put under normal grazing, the rapidity and vigor with which the climax bunchgrass, *Danthonia californica*, entered the space vacated by the removal of Klamath weed by beetles of the genus *Chrysomela* (= *Chrysolina*), promises much for the more favorable locations in Humboldt and possibly Mendocino, Trinity and Siskiyou counties in California.

The initiation of quantitative studies designed to follow the pattern of vegetational changes and the correlated beetle

populations was reported by Huffaker and Holloway (1949).

A brief review of an important survey of these counties by Davy (1902) indicates:

1) The climax grass cover in this area probably consisted of *Danthonia californica* as the most important component. Other bunchgrasses such as *Stipa*, *Melica*, *Elymus*, *Poa*, and *Festuca* were represented, as were important associated forage species such as *Trifolium* spp. (annual and perennial clovers), *Lathyrus* spp. (wild pea vines), and *Wyethia* sp. (wild sunflower).

2) There were important early changes, apparently beginning with invasion of the region by such introduced annuals as *Erodium cicutarium* (filaree) and *Avena fatua* (wild oats), later followed, as a result of still heavier stocking, by *Hordeum gussoneanum* (foxtail), *Festuca myuros* (rat-tail fescue), and *Bromus hordeaceus* (soft chess), and still later by the appearance of weedy arrivals during the last years of the past century, such as *Erodium moschatum* (musky filaree), *Bromus rigidus* (broncho grass), *Hordeum murinum* (foxtail), *Centaurea melitensis* (tactaloti), *Hypochoeris glabra* (hawkbit), and *Medicago hispida* (bur-clover). The latter species and the filaree are considered of definite forage value.

Some comparison of Davy's survey with the present quantitative results may be worthwhile. For example, *Hypochoeris glabra* was at that time making its appearance, but now is a definite pest. Also, *E. cicutarium*, the filaree which thrived prior to his study, is definitely not the species of *Erodium* now most common in either that area or at the

¹ Presented in general terms, with slides, at the Western Section Meeting of the Ecological Society at Salt Lake City, June 22, 1950.

The general project is under the coordinating supervision of J. K. Holloway and is a co-operative one under the direction of Professor H. S. Smith of the Division of Biological Control, University of California and C. P. Clausen of the Bureau of Entomology and Plant Quarantine of the U. S. Department of Agriculture.

The author wishes to express appreciation for the cooperation and assistance given this work by the Division of Agronomy of the University of California, and to acknowledge particularly the help of Professor Ben A. Madson and A. H. Murphy.

The detailed program of importation of the beetles, their distribution to the Klamath-weed-infested areas and the general progress of control of the weed, as distinct from this study of the associated vegetational changes in the specific study areas, is reported by Holloway and Huffaker (1951).

Loomis study locality in Placer county. *E. botrys* has entered and successfully occupies large areas. This latter species does not compete well with Klamath weed, but occupies sites on the drier side of the Klamath-weed moisture tolerance limits, whereas *Danthonia* holds out in locations too water-logged for the weed during winter. With disappearance of Klamath weed, filaree may have opportunity of some increase, but it is not an important constituent on the best ranges, at least in this Humboldt County area.

While soft chess was considered by Davy to be definitely secondary to fox-tail or rat-tail fescue in 1900, the reverse is overwhelmingly true today. Foxtail and rat-tail fescue, like *E. botrys*, appear to reach their maximum development on the drier or more over-grazed ranges, or on those with gravelly, shaly soils, steep slopes and rapid run-off and percolation. This fact, together with the fact of a gen-

eral increase in *Danthonia* where Klamath weed is brought under control, supports the view that more forward-looking range management is practised today than was so in the early days of land exploitation in this region. Time alone will answer the question as to whether the maximum is to be achieved from the removal of Klamath weed. It is hoped that the closely coordinated range management program of the Division of Agronomy of the University of California may encourage the ranchers to a wise program of range improvement and utilization.

No mention was made by Davy of Klamath weed, which is known to have appeared on a few ranches in the region at about that time. This weed occupies land of marked diversity in soil structure, chemical composition, exposure, slope, and moisture content. However, on gravelly or shallow soils, or on very steep



FIG. 1. Dense stand of climax, highly palatable bunchgrass, *Danthonia californica*, which appeared subsequent to removal of Klamath weed by imported beetles near Blocksburg, California. Note the heavy seed production.

slopes where moisture-retention qualities are poor, it develops a scattered cover of rather dwarf plants reaching a stature of only 5 to 6 inches during dry years. On such locations it is never wholly dominant and interferes only moderately with the rather low grazing value of such lands. At more favorable locations it develops stands so dense and vigorous that all forage plants disappear and the land is of little or no value for grazing.

It is in these latter locations that it has for many years occupied land which is capable of producing the principal climax species, *Danthonia californica*. As discussed under the "Blocksburg site" and shown in Figure 1, this perennial bunchgrass has formed such a dense cover as to resemble a turf-forming species in the area of the field first cleared by beetles. Observations in the Blocksburg-Fort Seward-Alder Point triangle as a whole reveal its general occurrence there, and removal of Klamath weed by such a factor as these beetles, may open up thousands of acres to return of this fine forage species.

It should be noted that such biological control agents are strictly selective weed killers. No pressure at all is exerted on the desirable forage plants. On the contrary, the opportunity for increase of good forage species is greatly magnified, since their most aggressive competitor, Klamath weed, is removed from the scene. When used to reduce Klamath weed infestations, sheep tend to feed more heavily on the palatable species than on the weed, and control in this manner must surely result in a seriously overgrazed condition unless done according to an extremely judicious procedure of timing, the requirements of which are not yet fully known. Some ranches adjacent to others heavily infested with the weed have been kept relatively free by use of very heavy stocking. In some such cases, depletion of ranch values is proceeding at a startling rate. On the other hand, the Division of Agronomy of the University of California has information indicating

that judiciously-timed sheep grazing, coupled with suitable non-grazing periods, may encourage return of a reasonably good grass cover, even *Danthonia californica* in cases.

METHODS

The methods of study are the same as those reported by Huffaker and Holloway (1949: 169), except as explained in the present text.² A few remarks regarding the plant sampling frame are pertinent. The frame is essentially a table $\frac{1}{4}$ sq. meter in area and having 28 brass rods as micro-plot designators (Huffaker, in press). The species of greatest development within a radius of 1 inch (all levels considered) is recorded at each rod point. While no claim is made that this technique is a critically sound procedure for approximating frequency, dry weight, yield, abundance or any other such concept, it does give a rapid determination of the dominant plants on such a range and does so with a considerable degree of sensitivity to species which may be dominant only over small micro-areas of a general position. It is felt that where extreme accuracy is not required, the method is applicable for use in following gross patterns of low, herbaceous, range plant changes. However, it does not accurately reflect the relative importance of a given species from year to year, since during a given year another larger, more vigorous plant may occupy the space along with it, while during another year it may occupy the same space alone and at essentially the same density. The method reflects what is implied—not density or percentage cover, but the proportions of micro-positions (two inches in diameter) dominated by the different species.

² The nomenclature followed for the California plants is that of Jepson, "A manual of the flowering plants of California," 1925. The author wishes to express his thanks to Mrs. Margaret K. Bellue of the California State Department of Agriculture and to staff members of the Herbarium, University of California, for making some of the plant determinations.

RESULTS

Action of beetles

There is unimpeachable evidence that the only important factor contributing to the destruction of the weed in these areas was the action of the beetles. Holloway and Huffaker (1951) review the general observations and mechanism of control in some detail, as well as the waves of progression from the release-centers outward, in some cases for a distance of several miles. As substantiation of the point with respect to the three study-areas herein reported, Figure 2 shows: 1) the rapid decline of the weed at each of the three locations, 2) the associated mature insects issuing at the yearly intervals for each generation, and 3) the decline of the beetles themselves as a result of the sudden depletion of their own food supply. The size of the mature brood, however, is an indication of *destruction to come* rather than that previously accomplished. This is because the larvae of the following generation represent the actual controlling factor. Only rarely do these occur in numbers *just sufficient* to control the weed and yet have adequate food to mature. Intra-specific competition usually reduces their numbers prior to maturity to a very small proportion of those which accomplish the necessary weed destruction. Considering each range area as a whole, it is seen that the largest mature populations were recorded in 1948, although the larger weed areas were destroyed by the *expended* larvae in 1949.

The data of Huffaker and Holloway (1949: Fig.-1) show that the weed retained essentially its original vigor in 1948 in all the sampled distance zones arranged outward from the original places of beetle release, except the center ones in which the weeds were destroyed by the beetles. Consideration of the present Loomis data, Figure 3, reveals the zone-by-zone pattern of weed destruction. The central zone was completely destroyed in 1948, and the beetles, present there since 1946, destroyed the weed, and most of the

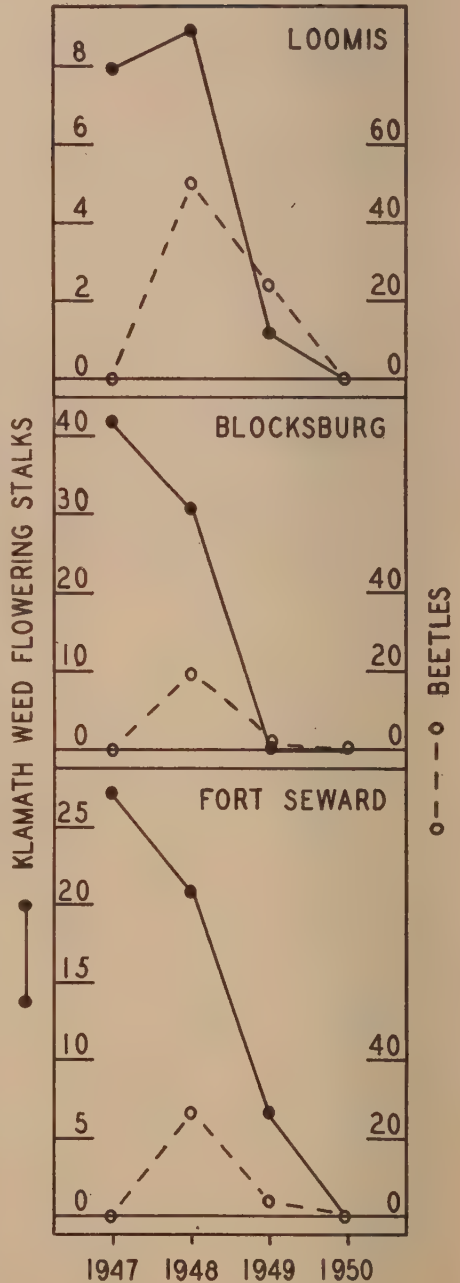


FIG. 2. Flowering stalks of Klamath weed and maturing beetles per quadrat of $\frac{1}{4}$ square meter for the years 1947 through 1950 at Loomis, Blocksburg, and Fort Seward, California.

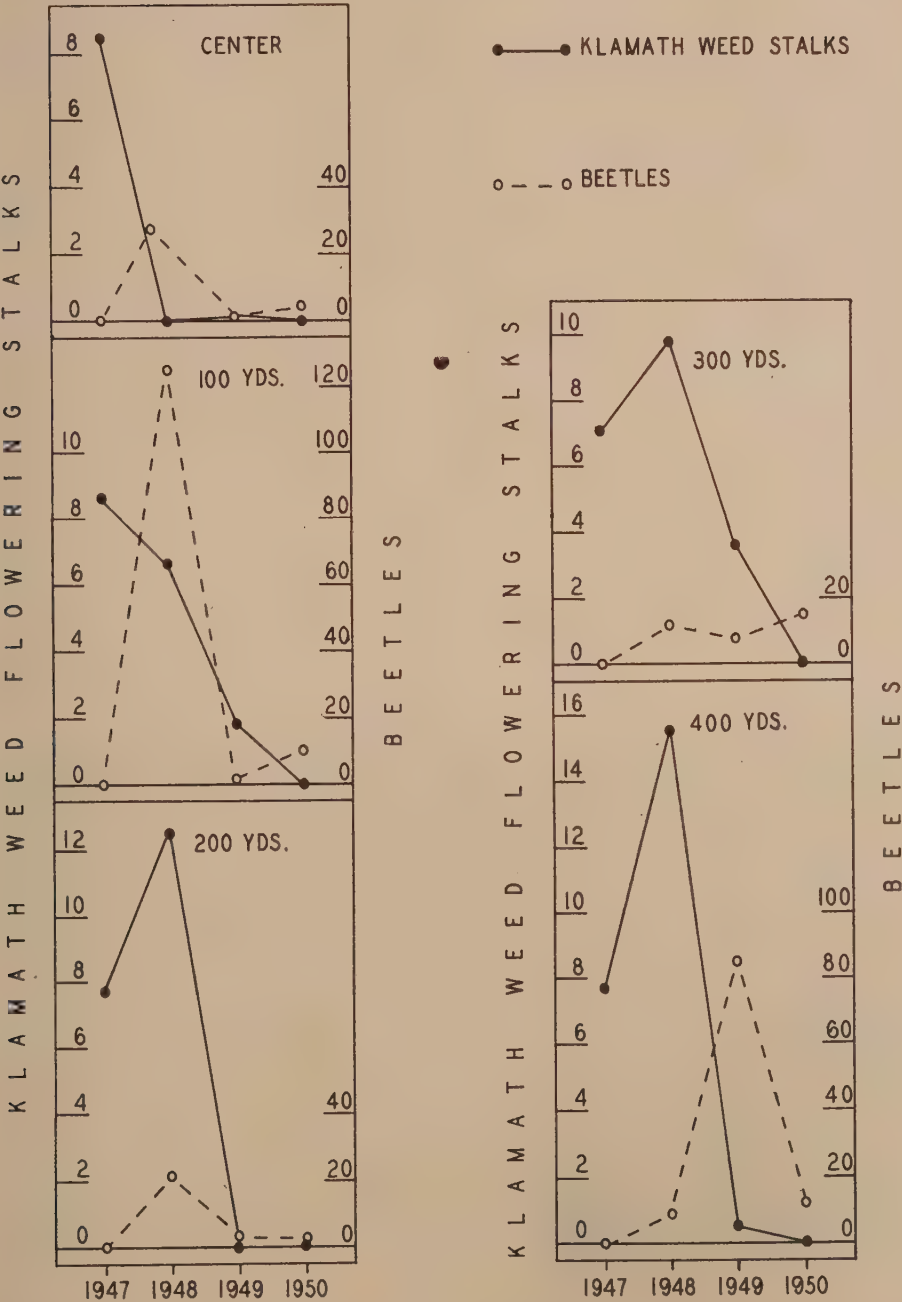


FIG. 3. The zone-by-zone pattern of reduction in Klamath weed flowering stalks and the corresponding maturing beetle populations per $\frac{1}{4}$ sq. m. quadrat at the Loomis beetle site for the years 1947 through 1950.

beetles died of food shortage the same year (hence, the emerging population was lower than at the 100-yard distance from the original center of beetle release). The zone at the 100-yard distance had a low density of extremely tall, vigorous weeds, and, although a large beetle population was present, only scattered plants were destroyed. The decline is shown to have been gradual. The same was true in 1949. The vast majority of the larvae died from starvation after completely defoliating the plants during a long winter period of no weed growth. A small proportion of weeds was able to recover and produced flowering stalks in July. This was also the pattern at the 300-yard zone. In both these zones the persistence of a few of the weeds at the end of the beetle period in 1949 permitted a slight resurgence of mature beetles in 1950. The larval counts (begun that year) showed that the numbers of immature stages present were far in excess of the adult populations shown in the present illustrations. Only at the

400-yard zone did the *effective* population in 1949 result in a noticeable peak of the *mature* population. This was one of the cases of a favorable balance for the beetles between their numbers and the amount of food available. It is from such areas as these, always present at one area or another along the periphery of a field undergoing control, that the hundreds of thousands of beetles intended for distribution to new weed areas are swept into pails and cartons.

Figure 4 is also a striking documentation of the removal of weeds by beetles in both the central and 200-yard zones at Blocksburg in 1948 and 1949. The beetle wave was so intense in 1948 at the margin of advance that all living weeds were devoured completely by the hungry adults as they moved onward. This produced the clearly-indicated boundary between the area cleared in 1948 and that cleared in 1949. The picture (Fig. 4) was taken in late May (1949), at which date in 1947 the entire field showed a very heavy



FIG. 4. Ranchers inspecting biological control results in late May 1949. The central zone (foreground) was cleared of Klamath weed in 1948. In 1947 the weed had been as dense in this zone as it appears to be here in the 200-yard zone just beyond the men, where the dark tone consists of a heavy stand of brown, dead, flowering stalks still standing immediately after destruction by the beetles. The 400-yard and 600-yard zones lie to the right, outside the photograph.

blanket of flowers. At that date in 1948, only the now-dead area beyond the mid-line was in heavy flower, and the foreground (central zone) was similar to the dark area of dead Klamath weed stalks here shown beyond the mid-line. In the central zone (cleared one year sooner) the old stalks had fallen down and been covered by a canopy of grass. The complete absence of Klamath weeds in flower, either in the zone that had been clear for two seasons or in the zone just cleared, testifies to the thoroughness of the beetles' work. The ranchers and hundreds of other observers have verified the sudden destruction of the weeds in this field which had been notorious for its Klamath weed for 25 years.

Such initial momentum is expected in a condition where a given host population has been permitted, in the absence of its effective biotic enemies, to reach levels beyond the point representing a normal balance between such a host population and the enemies which may control it. It is, of course, obvious to the ecologist that a weed under such biological control will undergo the oscillations characteristic of the density-dependent type of control. It is expected, therefore, that the control will not remain so complete, but will arrive at an oscillating balance. The overall acreage of weeds then is expected to be a small fraction of the present infestations, and the locations of weed patches should constantly shift from place to place, as each in its turn is eventually discovered by the beetles and destroyed. New weed patches will of course be established all the while.

A striking verification of the cause of weed removal was obtained in 1949 by treatment of two small rectangular plots with five per cent DDT spray. This was done to destroy the beetles themselves. Only those two small plots of the entire 50-acre field had weeds which survived the action of the beetles that year.

Loomis site

The pattern of Klamath weed removal by the beetle, *Chrysomela* (*Chrysolina*)

gemellata Rossi, at the Loomis location has been very gratifying. The tendency of the beetles to remain in an area of very low Klamath weed density and to further reduce it to an extremely low level is demonstrated. By the spring of 1948 the weed had been completely removed at the central zone, and had been reduced somewhat at the 100-yard, 200-yard and 300-yard distances. The weed density at the 400-yard distance was greater in 1948 than in 1947 (Huffaker and Holloway 1949). The beetles had to work over an area of increasingly scattered and isolated plants in 1949 and 1950. Due probably to differences in continuousness of the weed stands in the several zones, and the consequent greater reproductive realization, the weeds in the dense-weed area at the farthest extremity in this field were removed completely prior to clearance of two of the zones which were nearer the original beetle releases. Intense beetle activity was the direct cause of the destruction at all zones. By 1949 (Table I), an average of only 2.1 per cent of the original micro-plot positions were dominated by Klamath weed, compared to 26.1 per cent in 1947. However, the beetles continued their destructive action and reduced the weed to a level of only 0.1 per cent by 1950, demonstrating that, though their action is somewhat slower in a scattered stand compared to that in a range of almost continuous coverage (Blocksburg site), they are able to reduce the weed to a comparable extremely low level in either case.

An interesting observation relative to appearance of a reinfestation was made in 1949. Following removal of the weed by beetles at the central zone in 1948, the owner burned the area to destroy the dead weed stalks which persist in a field for one or two years or more. In late 1948 a heavy stand of Klamath weed seedlings developed as a result of the burn. By the spring of 1949, however, the beetles had re-entered the area and again destroyed practically every plant. In 1950 only a single living weed was sampled in the en-

TABLE I. Dominance of range plant species at micro-plot positions in quadrats at the Loomis beetle site, expressed as percentages of total positions*

Species	1947	1948	1949	1950
Klamath weed	26.1	15.4	2.1	0.1
Other important weeds:				
<i>Bromus rigidus</i>	6.1	6.9	10.3	7.1
<i>Amsinckia douglasiana</i>	1.9	1.0	0.0	0.9
<i>Hordeum gussoneanum</i> and <i>H. murinum</i>	0.1	0.9	0.0	0.0
<i>Eremocarpus setigerus</i>	0.0	0.0	1.4	0.0
Total for "Other weeds"	8.1	8.8	11.7	8.0
Legumes:				
<i>Lupinus</i> spp.	6.7	5.9	0.0	17.6
<i>Lotus</i> spp.	0.6	1.6	0.1	1.1
<i>Trifolium</i> spp.	0.1	0.0	0.0	3.8
<i>Medicago hispida</i>	0.0	1.3	0.0	0.6
Total legumes	7.4	8.8	0.1	23.1
Forage grasses:				
<i>Bromus hordeaceus</i>	14.3	48.3	50.9	36.3
<i>Festuca megalura</i> and <i>F. myuros</i>	6.0	11.2	9.0	0.4
<i>Aspris caryophylla</i>	1.0	2.4	0.1	0.3
<i>Briza minor</i>	0.0	0.0	0.0	0.3
Total forage grasses	21.3	61.9	60.0	37.3
Forbs:				
<i>Erodium botrys</i>	32.1	15.1	4.8	20.6
<i>Plagiobothrys canescens</i>	2.1	0.4	0.0	4.7
<i>Torilis nodosa</i>	0.1	1.7	0.3	0.4
<i>Geranium dissectum</i>	0.1	0.3	0.4	1.0
<i>Cerastium viscosum</i>	0.0	0.1	0.4	1.0
Miscellaneous species	0.8	0.7	0.2	0.9
Total forbs	35.3	18.3	6.1	28.6
Bare ground	1.7	0.7	18.7	3.1
Total forage species	63.9	89.0	66.2	89.0

* Based on records from 28 micro-plots per quadrat and 5 quadrats at each of 5 zones.

tire field, and this was in the zone which had had the lowest initial weed density.

The data of Table I show that there has been no consistent pattern of change in favor of certain species (other than the disappearance of Klamath weed) in this field as a result of the provision of new space by the removal of the weed. This may be expected from the results of Bentley and Talbot (1948) which indicated the high degree of variation in the annual plant vegetation of the California foothill region from year to year. This field was one of low initial Klamath weed density, and it would therefore be expected that

since important associated plants were already seeded in the area, there would only be increases in these proportional to the decreases in weed density.

As a rough means of checking on the changes in forage value, the several species were grouped into desirable and undesirable types. Klamath weed declined from 26.1 per cent to 0.1 per cent—a striking improvement because the space vacated was not taken over by plants equally objectionable (Fig. 5).

Buckthorn weed (*Amsinckia douglasiana*), perhaps the most objectionable of the undesirables listed, was present at a level

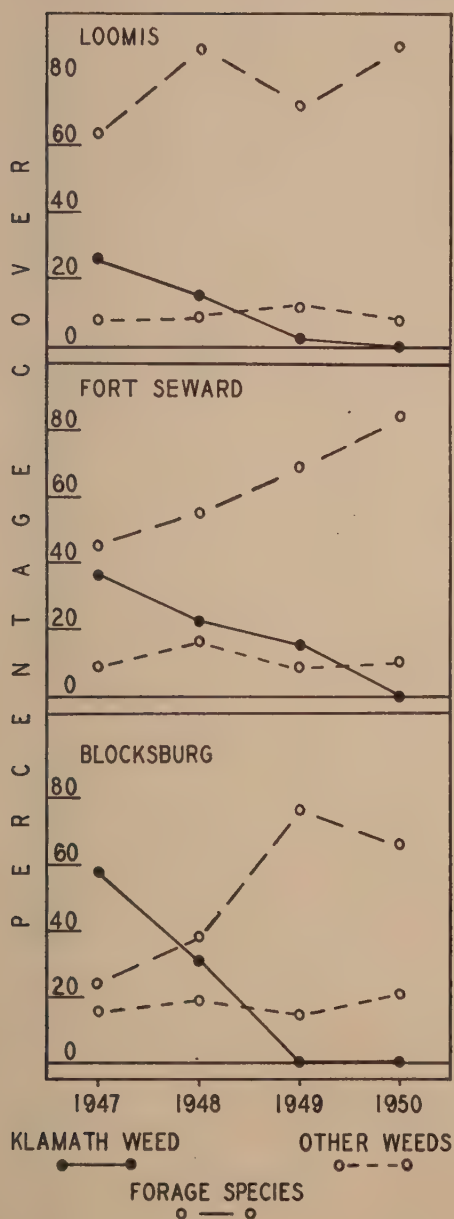


FIG. 5. Changes in cover by Klamath weed, other weeds, and desirable forage plants from 1947 through 1950, associated with destruction of Klamath weed by beetles in 1948, 1949 and 1950 at Blocksburg, Fort Seward, and Loomis, California.

of 1.9 per cent in 1947 and at 1.0 per cent, 0.0 per cent, and 0.9 per cent, respectively, in the years 1948, 1949, and 1950. General observations support these data as reflecting a slight decrease of this weed.

Rip-gut grass (*Bromus rigidus*) remained in about the same proportion to the total vegetation during 1948, at 6.9 per cent, increased very slightly in 1949 as a result of complete absence of grazing (to which this species is very susceptible) the previous year, and declined again in 1950 to approximately the same level it held in 1947.

The change in the weedy, annual, fox-tails (*Hordeum gussoneanum* and *H. murinum*, combined) has been negligible. These were almost absent in 1947, 1949 and again in 1950. They reached a level of 0.9 per cent in 1948, the most productive of the grass years during this study.

Turkey mullein (*Eremocarpus setigerus*) commonly associated with heavily overgrazed, soil-exposed ranges appeared in spots in 1949. The field was ungrazed in 1948 and this fact combined with favorable meteorological conditions contributed to an unusually tall and heavy vegetative cover which later fell over and blanketed the soil surface so heavily in spots that the usual winter annuals failed to establish, and early in the summer of 1949, such "bare" spots became suitable for establishment of *Eremocarpus*. Normal grazing and density of litter during 1949 and 1950 apparently contributed to development of a continuous competitive cover prior to the normal seed germination period for *Eremocarpus* in 1950, and it reappeared in the field in greatly reduced numbers.

In summary, there has been no increase in any of the other undesirable plant species in this annual-type foothill range as a result of the removal of Klamath weed by beetle action. Yellow star thistle (*Centaurea solstitialis*) is the one undesirable summer annual which may be expected to make some inroads in this range unless the past practice of light and

reasonably well-timed grazing is continued.

In contrast to the relatively static condition of other undesirable plants during the 3 years of Klamath weed decline, the more desirable forage plants have definitely increased (Fig. 5). There was a decline in miscellaneous forbs of variable forage value in 1948 and 1949, due to exceptionally good conditions of growth for grasses, in contrast to the forbs, in 1948, and possibly to the density of the litter cover as well as competition from the grasses, in 1949. The composition of forbs increased again in 1950 but was still definitely lower than in 1947. The outstanding improvement is shown in the relative change in legumes and desirable grasses, primarily the latter. These dominated at only 28.7 per cent of the micro-plot positions in 1947 and increased to 70.7 per cent, 60.1 per cent and 60.4 per cent, respectively, in the years 1948 to 1950, inclusive. Legumes, composed of species of *Lupinus*, *Lotus*, *Medicago*, and *Trifolium* competed well with the grasses and miscellaneous forbs only in 1950. Conditions for germination in the fall of 1949 must have been generally good for these types throughout many of the northern California counties, for increases in these forms were very noticeable in many of these areas.

Except for the "bare" (heavy litter) spots in 1949, the useful forbs, legumes and desirable grasses totalled around 88 per cent in the years 1948, 1949 and 1950 as against a figure of only 63 per cent in 1947.

Fort Seward site

The progress of weed control by a second, closely related species, *Chrysomela* (*Chrysolina*) *hyperici* Forst., has been in final effect identical with that by *C. gemellata* at the Blocksburg and Loomis sites. However, the progress was much slower. This species reached and cleared the 600-yard zone only in 1950, whereas clearance of areas equally distant by *C. gemellata* was accomplished

in 1948 at the Blocksburg site and in 1949 at the Loomis site. This species moved very slowly and ate the weed clean as it progressed. It moves in numbers only under very intense population pressure, and hence its potential multiplication is not realized by forging into new areas of abundant food until extremely large numbers have succumbed from starvation. However, this species is climatically out of synchronization over most of California (Holloway and Huffaker 1951). This field, also, was one of moderate, rather than heavy, continuous weed coverage in 1946 when the beetles were released.

By 1948 (Huffaker and Holloway 1949) the density of the weed in the central zone had been reduced from a level of 58.7 per cent to only 7.7 per cent, but all other zones that year had experienced no reduction in weeds due to beetle action. For the range as a whole, this resulted in a decrease from 36.6 per cent in 1947 to 22.5 per cent in 1948, Table II. The zone-by-zone data (not herein tabulated) show that the central zone was cleaned entirely of weeds in 1949 and the 100-yard zone experienced a weed reduction from 48.5 per cent in 1947 to 38.3 per cent in 1948, and to only 14.3 per cent in 1949. The 300-yard zone, beyond the advance of beetles at that time, increased in weeds from 8.7 per cent in 1948 to 12.8 per cent in 1949, while the 600-yard zone remained at the same weed level—at 35.2 per cent. By 1950, the beetles had gained momentum in numbers and consequent movement, and had destroyed the weeds in the distant zones. At the same time they had kept the previously cleared zones free from weeds.

Considering this range as a whole, the progress of weed control is shown by the yearly figures on weed dominance (Table II). A review of the specific data, by desirable and undesirable groups, reveals that the space vacated by the weed was taken over by desirable forage species. The undesirable, weedy species, com-

TABLE II. Dominance of range plant species at micro-plot positions in quadrats at the Fort Seward beetle site, expressed as percentages of total positions*

Species	1947	1948	1949	1950
Klamath weed	36.6	22.5	15.6	0.0
Other important weeds:				
<i>Hypochoeris glabra</i>	6.1	11.4	7.6	3.2
<i>Baeria chrysostoma</i>	0.6	3.8	0.7	2.7
<i>Hordeum gussoneanum</i> and <i>H. murinum</i>	1.5	0.0	0.0	1.9
<i>Agoseris heterophylla</i>	0.0	1.2	0.0	1.7
<i>Amsinckia douglasiana</i>	0.0	0.3	0.0	0.8
<i>Micropus</i> spp.	0.5	0.1	0.1	0.1
<i>Eremocarpus setigerus</i>	0.0	0.0	0.0	0.1
Total for "Other weeds"	8.7	16.8	8.4	10.5
Legumes:				
<i>Trifolium</i> spp.	2.3	6.4	0.0	17.4
<i>Lotus</i> spp.	0.1	2.0	1.7	11.6
<i>Lupinus</i> spp.	0.0	0.1	0.0	0.5
Total legumes	2.4	8.5	1.7	29.5
Forage grasses:				
<i>Bromus hordeaceus</i>	14.8	6.4	34.1	20.3
<i>Aspris caryophylla</i>	4.8	3.8	10.3	3.9
<i>Danthonia californica</i>	2.9	0.5	2.8	1.6
<i>Avena fatua</i>	4.7	1.7	0.8	0.6
<i>Festuca megalura</i> and <i>F. myuros</i>	2.3	1.0	2.4	0.6
<i>Briza minor</i>	0.1	1.9	0.0	3.6
<i>Elymus glaucus</i>	0.0	1.0	0.4	0.8
Total forage grasses	29.6	16.3	50.8	31.4
Forbs:				
<i>Erodium</i> spp.**	9.9	21.0	11.7	11.8
<i>Geranium</i> spp.***	0.5	1.4	1.3	3.6
<i>Orthocarpus</i> , <i>Cordylanthus</i> , <i>Castilleja</i>	0.8	2.2	0.1	2.3
<i>Linanthus bicolor</i>	0.1	3.3	0.3	0.8
<i>Galium</i> spp.	0.0	0.1	0.5	1.3
<i>Ranunculus</i> spp.	0.0	0.6	1.2	0.3
<i>Plagiobothrys canescens</i>	0.3	0.9	0.0	0.8
<i>Daucus carota</i>	0.0	0.1	0.0	0.6
<i>Cerastium viscosum</i>	0.0	0.0	0.0	0.6
Miscellaneous species	1.5	0.6	1.3	1.4
Total forbs	13.1	30.2	16.4	23.5
Bare ground	9.7	5.6	7.4	5.1
Total forage species	45.1	55.0	68.9	84.4

* Based on records from 28 micro-plots per quadrat and 7 quadrats at each of 4 zones.

** Nearly all *E. botrys* but *E. cicutarium* also present.*** Nearly all *G. dissectum* but other species also present.

posed primarily of *Hypochoeris glabra*, *Hordeum gussoneanum*, *H. murinum*, *Baeria chrysostoma*, and *Agoseris heterophylla* increased markedly only in 1948, as a result of assumption of the dominant position by *Hypochoeris glabra* following removal of Klamath weed in 1948 at the central zone. Davy (1902) considered this species a potentially serious

weed but at that time it had just entered the area. This species had been co-existent with Klamath weed as an inferior stratum in 1947. After more time had elapsed for other species to become adequately seeded, this prostrate form declined. It is seen, therefore, that the space vacated by Klamath weed has not been occupied by undesirable forms, even

though some such species were already present in the field.

A consideration of the data in Table II again shows that legumes, composed of species of *Lotus*, *Lupinus* and *Trifolium* increased markedly in 1950, competing well with grass and forb species at all zones that year. Grass species of variable forage value represented 29.6 per cent of the cover in 1947. These declined in 1948 to only 16.3 per cent, giving ground that year to such forbs as *Erodium botrys* due to poor development that year of *Bromus hordeaceus*, the principal grass component.

In 1949, *B. hordeaceus*, and consequently the grass species as a whole, utilized the space vacated by Klamath weed, but in 1950 gave ground to legumes rather than to the miscellaneous forbs as was the case in 1948.

The forbs generally have about doubled since 1947 on this range, thus accounting for a part of the space vacated by Klamath weed. The annual grasses during favorable years, may now reach a state of productiveness not possible prior to removal of Klamath weed by the beetles.

This range has comparable rainfall with the one at Blocksburg. Yet the perennial climax grass, *Danthonia californica*, has strikingly increased at the latter location, while there has been no such change in the grass cover at this location. This is undoubtedly due in part to differences in soil type and run-off potentialities. The Fort Seward site has been under moderate grazing, but the timing of the grazing period has not been practiced in such a way as to give an advantage toward seeding of the deep-rooted perennial grasses. Both *Danthonia californica* and *Elymus glaucus* were present on this range at favored locations when the beetle releases were made in 1946 but they have shown only slight tendencies to increase as the Klamath weed has been removed by beetles. Increase of *Danthonia* would be expected to be slower than at the Blocksburg site, but, never-

theless, if favored by delayed, reduced, or better-timed grazing, might take place with steadily mounting impetus.

Blocksburg site

Klamath weed was removed faster and the beetles, *C. gemellata*, moved much farther at this location than at any other location in the State. This is partly due to the perfect synchronization between the weed, the particular beetle, and the annual climatic trends. However, the presence of a large acreage of continuous, dense stands of food in this area is also considered to have been very contributive. As shown by Huffaker and Holloway (1949), the weed was completely removed at the central zone in 1948. Figure 4 shows the condition in June of that year when the beetles had advanced to a mid-line in the field and created a condition so striking as to represent a proof of their effectiveness that was questioned by no one who had followed the progress of the program. This condition has recurred again and again and been observed by many ranchers on their own ranges.

The Blocksburg site is in a location conducive to maximum improvement from a program of biological control of Klamath weed. In that area the soil is good and the rainfall favorable to development of perennial bunchgrass. There, the deep-rooted bunchgrass, *Danthonia californica*, was able to survive the local range practices for many years prior to entry of Klamath weed at the turn of the century. As pointed out by Sampson and Parker (1930) the perennial bunchgrasses of this region, because of their deep root systems and long growth cycles, were the last plants to yield their foothold to the weed. According to those authors the depth of the root system of *Danthonia* on these ranges is from 6 inches to a foot less than that of Klamath weed.

Figure 6 shows unclipped and clipped plants experimentally simulating degrees of beetle damage. The plant at the left



FIG. 6. Roots produced by: a) vigorous, undamaged Klamath weed plant, compared to b) one moderately clipped, and c) one severely clipped. Actual beetle feeding is even more destructive than this severe degree of "simulated injury."

(a) shows the massiveness of the root system of a normal, healthy Klamath weed plant, compared to (b) a plant which was kept clipped to a foliage production only 50 per cent that of the check "a," and to (c) a plant kept clipped to a level of about 12 per cent of normal, throughout the period of intense beetle feeding action (December to July) but not exposed to the beetles. This test was set up to learn whether even partial destruction by beetles could be expected to set in motion a competitive struggle between the weed and good range grasses which might prove favorable to the latter. A notable case of weed control by such indirect insect action is that of replacement of *Clidemia hirta* by desirable range types as a result of the weakening action

of an introduced thrips (Simmonds 1933). The initial stages in the biological control of Klamath weed, however, are now known to be the result of direct destruction of the host plants by the beetles. The competitive angle may be involved in the final oscillatory equilibrium and particularly in regard to re-establishment of seedlings in cleared areas.

The growth cycle of the weed, and hence its requirements, is almost identical with that of the bunchgrass. However, since the root depth of the weed exceeds that of *Danthonia*, and since its aerial growth is much taller, causing it to cast heavier shade over undergrowth, and since its seedlings have the ability to utilize the smallest available spaces for establishment, this weed eventually replaced even *Danthonia* except in seepage areas or along hard-beaten cattle paths where Klamath weed is at a disadvantage. In spots favorable to *Danthonia* this original climax cover maintained itself and was in a position to increase rapidly as the beetles removed the dominant Klamath weed.

At this site, not only has there been no increase in undesirable range species, but the most desirable of perennial range grasses has increased to a condition as sole dominant over sizeable portions of the field. Vigorous growth in the initially-established areas (Fig. 1) and appearance of young plants at all zones studied, promise much for the future on this range unless the Klamath weed beetles are unable to maintain their present efficacy as agents of weed control.

In 1946 and 1947 all the portions of the field shown in figure 4 had a complete and very heavy cover of Klamath weed—to a point of sole dominance in the usual sense. Beetles were placed in the foreground part (central zone) in 1946, and by 1948 they had completely destroyed the weed in the release zone (foreground). At the time the picture was taken in May, 1949, they had also killed the weeds at all the other distances sam-

TABLE III. Dominance of range plant species at micro-plot positions in quadrats at the Blocksburg beetle site, expressed as percentages of total positions*

Species	1947	1948	1949	1950
Klamath weed	57.6	31.1	0.0	0.0
Other important weeds:				
<i>Hypochoeris glabra</i>	12.9	15.4	11.7	18.8
<i>Plantago</i> spp.	1.7	2.4	0.7	0.5
<i>Rumex</i> spp.	0.4	0.4	1.5	1.0
<i>Chlorogalum pomeridianum</i>	0.3	0.4	0.3	0.4
<i>Bromus rigidus</i>	0.0	0.0	0.4	0.8
Total for "Other weeds"	15.3	18.6	14.6	21.5
Legumes:				
<i>Lotus</i> spp.	0.0	0.9	0.8	2.3
<i>Trifolium</i> spp.	0.8	0.8	0.1	2.9
Total legumes	0.8	1.7	0.9	5.2
Forage grasses:				
<i>Danthonia californica</i>	9.2	13.3	22.7	23.4
<i>Bromus hordeaceus</i>	4.9	10.1	18.5	16.2
<i>Aspris caryophylla</i>	5.9	3.7	23.6	7.1
<i>Agrostis hallii?</i>	0.5	1.5	2.3	1.1
<i>Briza minor</i>	0.0	4.3	0.3	2.8
<i>Panicum pacificum</i>	0.7	0.3	0.4	0.3
Total forage grasses	21.2	33.2	67.8	50.9
Forbs:				
<i>Galium</i> spp.	0.1	0.3	2.1	3.6
<i>Ranunculus</i> spp.	0.0	0.1	0.4	0.3
<i>Daucus carota</i>	0.5	0.1	1.2	0.0
<i>Prunella vulgaris</i> **	0.4	0.4	0.5	0.5
<i>Linanthus bicolor</i>	0.3	0.7	0.0	0.1
<i>Orthocarpus, Cordylanthus, Castilleja</i>	0.1	0.3	0.0	0.4
<i>Luzula, Juncus</i> , sedges	0.0	0.4	1.3	0.9
<i>Sisyrinchium bellum</i>	0.0	0.0	1.4	1.2
Miscellaneous species	0.7	1.1	1.0	3.0
Total forbs	2.1	3.4	7.9	10.0
Bare ground	3.5	12.4	8.8	12.8
Total forage species	24.1	38.3	76.6	66.1

* Based on records from 28 micro-plots per quadrat and 7 quadrats at each of 4 zones.

** Jepson uses *Brunella vulgaris* L., but Linnaeus originally named the genus *Prunella*.

pled and grass had invaded the release zone which was cleared the previous year. The control area, overwhelmingly dominated (not exclusively) by natural movements from this one release, was increased to nearly 100 square miles in 1950. The dark area beyond the men in Figure 4 is the heavy stand of dead weed stalks which was killed in 1949 but had not at that time fallen over and been covered by the invading grass. The density of the weed for all four zones (two zones are outside the photograph)

in 1947 was only 57.6 per cent, Table III. This is partly because even in a quadrat of complete Klamath weed dominance, a small number of micro-plot positions are always dominated by other associated species. The density of 57.6 per cent for the entire field was reduced to 31.1 per cent in 1948 and to a zero level in 1949, a level which was maintained in 1950 in spite of the appearance of many seedlings which were unable to become established, due both to competition from other plants and to continued beetle pressure.

CONCLUSIONS

The progress of the biological control of Klamath weed has been gratifying. *Danthonia californica*, the climax bunchgrass of the Northwestern California counties prior to overutilization by grazing animals, has returned as the sole dominant in certain areas cleared of weed by the beetles in 1948. Maximum benefits from use of this method may accrue to those ranches which have suffered the least basic deterioration and which are located most favorably as to soil and climate. In the Blocksburg region, the climax bunchgrass type may be encouraged by reasonably good management practices to reoccupy the land as Klamath weed is removed. Many highland ranges in the Northwest counties occupy a position somewhat intermediate between the Blocksburg site and typical conditions for the Sierra foothill counties. The very best management, preceded by research to ascertain what this shall be, will be necessary in order to achieve a climax vegetation on the intermediate lands. There appears to be little indication that the perennial bunchgrass state may be achieved in the Sierra foothill region. Annual grasses, dominated by *Bromus hordeaceus* (soft chess), *Erodium botrys* (filaree) and various species of clovers, lotus, lupines and miscellaneous forbs are admirably adapted to the drier conditions and shorter growth seasons of that region and, in addition, produce good forage.

It was demonstrated that no essential increase in other weedy species at any of the study-localities occurred following removal of Klamath weed from those ranges. The exact pattern of assumption of space by other plants as it is vacated by the weed cannot be ascertained by a short-time study, particularly because of the normally marked variability of the annual-plant type from year to year.

The control area resulting from the Blocksburg beetle release reached a size of approximately 100 square miles in

1950, and may well approach county-wide proportions within two more years.

The return of the weed will be slow and hazardous, as it will be under constant pressure from the existent vegetation and the beetles. According to Bellue (1945) Klamath weed seeds may remain viable in the soil for at least 10 years. However, it is presumed that the total store of viable seeds on the surface (and thus available for germination) may be depleted rather rapidly following clearance of large tracts. The final equilibrium would be expected only when viability of the huge reservoir of seeds from the unnaturally extensive stands of former years has been depleted. It is hardly necessary to state that extermination is neither possible nor desirable. The rapidity and efficacy with which the beetles discover and destroy ever-appearing patches of weed will determine the final success of the program.

SUMMARY

Changes in the coverage of range plants at 3 study-localities as associated with destruction of Klamath weed (*Hypericum perforatum*) by imported insect enemies were studied for a total of five seasons. The progress of this research on the biological control of a weed covering this 5-year period is brought up-to-date, summarized and documented with graphs, pictures and lists of plant species in quadrats at three localities in California. A previous, preliminary paper (Huffaker and Holloway 1949) reported the methods used and the general outline of the study, and reviewed similar representative examples of such applied ecology in other parts of the world.

A comparison of the present quadrat studies was made with results of studies by Davy (1902) concerning the range plant history of the Northwestern counties of California. Present observations and the detailed studies on a limited scale add to the evidence that the perennial bunchgrass, *Danthonia californica*, represented the principal dominant of the

original climax grass cover of the region. The predominant grasses at the time of his observations appeared to have been *Hordeum gussoneanum* (annual foxtail, or small barley grass) and *Festuca myuros* (rat-tail fescue), with *Bromus hordeaceus* (soft chess) occupying a definitely minor position. The positions of these 3 species today have been reversed, with *Bromus hordeaceus* now overwhelmingly predominant over most of the annual-plant ranges. *Erodium cicutarium* (filaree) had occupied the region earlier, along with *Avena fatua* (wild oats), and then been replaced by the aforementioned annual grasses. Another species of filaree, *Erodium botrys*, is now a dominant on many of these ranges. Only one of the weedy forbs considered by Davy as dangerous has become a definite problem on these ranges. This is *Hypochoeris glabra* (hawkbit) which grows as a very tight rosette, successfully crowding out close competition.

Danthonia californica has returned as sole dominant in one area which now has been free of Klamath weed for three seasons. The pattern of weed disappearance was shown to have been the direct result of beetle action. At the more favorable locations this succession may be expected over large acreages. Results of range plant changes and the correlated mature beetle populations were discussed for each of the three study-localities. There has been no increase in serious weeds asso-

ciated with removal of Klamath weed. Essentially all the space vacated by the weed has been occupied by the fair-to-good forage species of each area. The control area at one of the release sites has now reached an extent of approximately 100 square miles. The final control will probably be at a much lower but oscillating level of weed density.

LITERATURE CITED

- Bellue, Margaret K. 1945. Weed seed handbook, Series III. Bull. California State Dept. Agr. 34 (3): 116-123.
- Bentley, J. R., and M. W. Talbot. 1948. Annual-plant vegetation of the California foothills as related to range management. Ecology 29: 72-79.
- Davy, Joseph Burr. 1902. Stock ranges of Northwestern California: Notes on the grasses and forage plants and range conditions. U.S.D.A. Bur. Plant Ind., Bull. 12: 1-81.
- Holloway, J. K., and C. B. Huffaker. 1951. The role of *Chrysolina gemellata* (Rossi) in the biological control of Klamath weed. Jour. Econ. Ent. 44: in press.
- Huffaker, C. B. In press. Quantitative studies on the biological control of St. John's wort (Klamath weed) in California. Proc. Seventh Pacific Sci. Cong. Roy. Soc. New Zealand 4: in press.
- Huffaker, C. B., and J. K. Holloway. 1949. Changes in range plant population structure associated with feeding of imported enemies of Klamath weed (*Hypericum perforatum* L.). Ecology 30: 167-175.
- Sampson, A. W., and K. W. Parker. 1930. St. Johnswort on range lands of California. California Agr. Exp. Sta. Bull. 503: 1-48.
- Simmonds, H. W. 1933. The biological control of the weed *Clidemia hirta* D. Don. in Fiji Bull. Ent. Res. 24: 345-348.

THE RELATION BETWEEN LEVEL OF POPULATION AND PREGNANCY OF NORWAY RATS¹

DAVID E. DAVIS

The Johns Hopkins University School of Hygiene and Public Health, Baltimore, Maryland

It has been established that, like many other species, a reduced population of rats increases till it reaches an asymptotic value (Emlen, Stokes, and Winsor 1948; Davis, unpublished manuscript). As the population approaches the asymptotic value, a number of changes occur in the forces of reproduction, mortality, and movement. This paper attempts to analyze the effects of population size on the reproductive rate. A preliminary summary (Davis 1949) indicated that a sub-asymptotic population has a higher pregnancy rate than has an asymptotic one. Additional data will be analyzed here.

The basic procedure was to remove Norway rats (*Rattus norvegicus*) from a stationary population of known number, determine reproductive rates and then, 2-3 months later, remove another sample from the now increasing population. Usually about one half of the rats was removed at each trapping. The rats were living in the yards, alleys, basements and garages of residential areas of Baltimore. The rats were captured in box traps and brought to the laboratory for autopsy. The populations were estimated by the method of Emlen, Stokes, and Davis (1949) which can detect changes of more than 10 per cent. In addition to the stationary and increasing populations, the numbers in some blocks were decreasing because of environmental factors beyond the control of the experiment. Thus, for analysis, the populations were classified

as stationary, increasing, or decreasing. The trapping was done between May, 1947, and May, 1949, in a total of 62 blocks and provided a total of 833 adult (i.e., with perforate vagina) females.

When the prevalences of pregnancy in stationary, increasing, and decreasing populations of rats were compared (Table I) differences of considerable significance ($P < 0.05$) were found between stationary and increasing populations and also between stationary and decreasing populations. Additional information can be obtained by dividing each of the three categories into high (spring) and low (other seasons) breeding periods in accordance with the data on seasonal distribution of pregnancies (Davis 1951). Actually there is a secondary peak of pregnancy in the fall but only a negligible number of rats was caught at that season. The differences in pregnancy shown in Table I show a significant ($P = 0.05$) difference between the low and the high reproductive season for rats from increasing populations but no significant differences in the others. The interpretation of these differences is that an increasing population had a great increment of pregnancy (increase of 60.0 per cent) in the breeding season in contrast to the other populations. Thus the increasing populations not only have a higher pregnancy rate but also increase in the period of high reproduction.

Additional data are available from a farm near Baltimore. In March, 1947, the population was estimated to be 430 rats, and 122 rats were trapped. In April the population was estimated to be 280 rats and 54 rats were trapped from the now decreasing population. In March 14.4 per cent of 63 adult females (rats

¹ Contribution from the Division of Vertebrate Ecology of the Department of Parasitology, The Johns Hopkins University School of Hygiene and Public Health. This investigation was supported in part by a research grant from the Division of Research Grants and Fellowships of the National Institutes of Health, U. S. Public Health Service.

TABLE I. Comparison of pregnancy and lactation rates

		Population level		
		Stationary	Increasing	Decreasing
Prevalence of pregnancy	Adult females	442	263	162
	Per cent pregnant	18.6	29.8	30.9
	<i>P</i> value (with stationary)	—	0.008	0.027
Low breeding season	Adult females	174	194	66
	Per cent pregnant	23.1	26.0	32.7
High breeding season	Adult females	268	69	95
	Per cent pregnant	14.4	41.6	25.3
Prevalence of lactation	Adult females	439	254	162
	Per cent lactating	43.0	42.4	39.9
Embryos	Pregnant rats	86	73	45
	Mean embryos	10.34	10.29	9.93
	Standard deviation	2.5	2.6	2.3
Incidence of pregnancy		3.8	6.1	6.3
	Upper limit (+2 S.E.)	4.3	7.2	7.8
	Lower limit (−2 S.E.)	3.2	4.9	4.8
Incidence of lactation		4.3	4.2	4.0
	Upper limit (+2 S.E.)	4.8	4.9	4.8
	Lower limit (−2 S.E.)	3.8	3.6	3.2

with perforate vagina) were pregnant and in April 48.3 per cent of 29 adult females were pregnant. The difference is significant ($P < 0.0005$). Data from three subsequent years show that there is no seasonal difference in pregnancy rates between March and April and hence it is believed that the difference in 1947 is due to change in population.

Although the comparison of pregnancy presents a logical relation to population size, a comparison of the prevalence of lactation (Table I) shows no differences among the three categories of population. Analysis of lactation by length or weight groups shows practically the same prevalences for each size class in all three population categories. This result suggests that there is a greater mortality of young at or shortly after parturition in the increasing populations than in the stationary populations, thereby giving about the same prevalence of lactation. The same situation occurred on the farm. In March, 1947, 25.4 per cent of 63 adult females were lactating and in April, 38.0 per cent of 29 were lactating. The difference is not significant.

The amount of loss of entire litters may be estimated by a comparison of the annual incidence of pregnancy and of

lactation calculated by the formulas $I_P = \frac{365P}{18} = 20.3P$ and $I_L = \frac{365L}{36} = 10L$

where I_P is the annual incidence of pregnancy, I_L is annual incidence of lactation, P is the prevalence of pregnancy, L is the prevalence of lactation, 365 is the number of days in a year, 18 is the number of days during which pregnancy can be macroscopically determined and 36 is the number of days during which lactation can be determined. The upper and lower limits at a confidence level of $P = 0.05$ may be calculated by adding or subtracting 2 standard errors ($S.E. = \sqrt{pq/n}$) to the values for P and L . From these calculations (Table I) it is possible that a loss of complete litters of about 31 per cent (i.e., from 6.1 to 4.2) may occur in the increasing populations although if we compare the lower limit of pregnancy (4.9) and the upper limit of lactation (4.9) then no loss is indicated. The meeting of the limits occurs for decreasing populations so that one hesitates to conclude that the apparent loss (6.3–4.0) really occurs. The over-lapping of the limits for stationary populations and the "gain" of litters from pregnancy to lactation (3.8–4.3) suggest that the loss of complete litters must be slight.

A comparison of the number of embryos in the three categories of populations showed no differences (Table I) in relation to population level.

These results indicate that although the increasing populations have a higher prevalence of pregnancy, the number of young weaned or at least being suckled is about the same as in stationary populations in city blocks. The increase in numbers of rats in increasing populations must come therefore from a better survival of young rats after weaning. No logical explanation is apparent for the increase in pregnancy of a decreasing population.

SUMMARY

Increasing and decreasing populations of Norway rats have significantly greater prevalences of pregnancy than do station-

ary populations. However, the prevalence of lactation is about the same at the three levels. Hence, there must be a greater parturitional mortality in the increasing populations and also a greater survival of young to produce the increase.

REFERENCES

- Davis, David E. 1949. The role of intra-specific competition in game management. Trans. 14th N. Am. Wildlife Conf.: 225-231.
- . 1951. A comparison of reproductive potential of two rat populations. Ecology, 32: 469-475.
- Emlen, J. T., A. W. Stokes, and C. P. Winsor. 1948. The rate of recovery of decimated populations of brown rats in nature. Ecology, 29: 133-145.
- Emlen, John T., A. W. Stokes, and David E. Davis. 1949. Methods for estimating populations of brown rats in urban habitats. Ecology, 30: 430-442.

THE RELATION BETWEEN LEVEL OF POPULATION AND SIZE AND SEX OF NORWAY RATS¹

DAVID E. DAVIS

The Johns Hopkins University School of Hygiene and Public Health, Baltimore, Maryland

In an attempt to analyze in nature the mechanics of populations the relation of a number of population characteristics to the population level was investigated. This paper compares the size and sex of Norway rats (*Rattus norvegicus*) with the level of the population. The rats were trapped in residential areas of Baltimore in blocks with known histories and populations as estimated by the sign method (Emlen, Stokes, and Davis 1949). The trapped rats were removed from the blocks, measured, and autopsied in the laboratory. In a preliminary report (Davis 1949) it was indicated that rats in increasing populations increase rapidly in size. Additional data are presented here.

The results of the analysis according to weight and length are presented in Table I. This table includes males and females because there were no significant differences in sex composition among the three types of populations. Thus although the females weighed significantly less than the males, they comprised the same proportion of each type of population. It is at once apparent from the table that each weight and length class composes approximately the same percentage of the stationary, increasing, and decreasing populations. There are no significant differences even at the $P = 0.05$ level.

A subdivision of the rats by sex and according to breeding season (high and low periods) however, revealed a few differences that may be of interest. These divi-

sions of the breeding season were based on the prevalence of pregnancy. Although rats breed throughout the year, maxima occur in spring (March-June) and fall (September-October). The rats therefore were divided according to high breeding season (months as above) and low breeding season (other months). Analy-

TABLE I. *Relation of population level to weight and head + body length of rats*

	Population level		
	Stationary	Increasing	Decreasing
Weight 0-99 g	184	78	53
Per cent	16.6	13.3	13.9
100-199	167	90	66
Per cent	15.1	15.3	17.4
200-299	182	118	43
Per cent	16.4	18.3	11.3
300-399	264	173	92
Per cent	23.8	26.8	24.2
400-499	230	133	94
Per cent	20.8	20.4	24.7
500+	82	53	32
Per cent	7.4	8.2	8.4
Total rats	1109	645	380
Length 80-99 mm	49	15	18
Per cent	4.5	2.4	4.7
120-159	191	86	52
Per cent	17.5	13.6	13.7
160-199	174	139	62
Per cent	15.9	22.0	16.4
200-239	534	313	174
Per cent	48.8	49.4	46.0
240-279	143	81	73
Per cent	13.1	12.8	19.3
Total rats	1091	634	379

sis of these divisions revealed some suggestive results. The males (Table II) in the period of low reproduction (winter and summer) were heavier in the decreasing population than those in the increasing but probably not than those in the stationary (see P values). Furthermore, the males were longer in the decreasing populations than those in either increasing or in stationary populations. No category of fe-

¹ Contribution from the Vertebrate Ecology Division of the Department of Parasitology, The Johns Hopkins University School of Hygiene and Public Health. This investigation was supported in part by a research grant from the Division of Research Grants and Fellowships of the National Institutes of Health, U. S. Public Health Service.

TABLE II. *Comparison of size differences of male rats in low reproductive season*

Population	Mean size	Standard deviation	Rats
1 Decreasing	344.4 g	136.5 g	88
2 Increasing	311.3 g	153 g	241
3 Stationary	318.8 g	142.0 g	235
4 Decreasing	216.0 mm	38.6 mm	87
5 Increasing	205.1 mm	35.0 mm	239
6 Stationary	200.4 mm	43.4 mm	250
Comparison		Value of <i>P</i>	
1 and 2		0.0574	
1 and 3		0.1096	
4 and 5		0.0214	
4 and 6		0.0019	

males in either high or low reproductive season differed from other categories. While these data are only suggestive they agree with the rather logical hypothesis that in decreasing populations the largest individuals survive, perhaps because of their high rank in the social order.

The interpretation of the data in Table I which show a similarity in size composition in stationary and increasing populations is based on the assumption that an increasing population must have a larger proportion of chronologically young rats than does a stationary population. This seems obvious because the population in a block was reduced by removing about half the rats. Then two to three months later another sample of the now increasing population was removed. It is evident that the increase must come from the production of young rats since immigration is negligible (Emlen, Stokes, and Winsor 1948). It is suggested that since the younger rats weigh the same as the older rats, therefore the younger rats must have grown more rapidly in the increasing populations than in the stationary populations. That the rats of the decreasing populations also weigh the same may merely reflect the high mortality of young individuals which would compensate for a stability or even loss in weight of the survivors.

An interesting relation was found on a farm on which the rat population declined in a year from about 1100 rats to about 400

due to a gradual reduction in food and shelter. The population was apparently always at the capacity of the farm to support rats. Analysis of the weights of 2,181 rats captured during this period showed no relation to changes in population although there were changes in average weight due to a large number of young in the period of high reproduction.

Data have been analyzed for length of rats (body + head) and size (either weight or length) at which 50 per cent of the rats attain the characters (1) eruption of third molar tooth, (2) descent of the testes, or (3) perforation of the vagina. These criteria showed the same general relation as was presented above for the weight of the rats. The data are not presented here in detail because these criteria are all merely another example of growth characters and would not be expected to differ from weight in the aspects discussed in this paper.

Alternative explanations of the similarity of size composition in stationary and increasing populations should be considered. There is no reason to think that differential trapping can explain the difference but it is possible that high death and birth rates are responsible. If birth and death rates are very high then there will always be a rapid replacement of mature rats by young rats. The removal of rats might not increase the death rate enough to alter the age composition to an extent that is measurable by present methods. However, it seems likely that the removal of half the rats in a block would increase the death rate enough to be

TABLE III. *Sex ratio in relation to population level*

Sex	Population level			Total rats
	Stationary	Increasing	Decreasing	
Male rats	539	335	184	1058
Per cent male	48.6	51.8	48.4	49.5
Female rats	570	310	196	1076
Total rats	1109	645	380	2134

detected. Therefore the explanation that there was a rapid increase in growth is preferred.

The sex ratio (Table III) shows no differences (P is always more than 0.05) in relation to population level. Nor is any of the ratios significantly different from 50 per cent. However, a difference of some significance ($P = 0.02$) occurs between the percentages of males in the high and low reproductive periods. In the high period 47.0 per cent of 1,051 rats were males while in the low period 51.9 per cent of 1,085 rats were males. A biological significance of this relation is not apparent and the difference should not be considered as established.

SUMMARY

Analysis of the weight composition of 1,109 rats from stationary populations, 645

rats from increasing populations, and 380 rats from decreasing populations showed no differences. It is suggested that the rats in the increasing populations must have gained weight more rapidly than those in the stationary populations since they must have been chronologically younger. There was no difference in sex ratio among the three levels nor any difference from 50 per cent males.

REFERENCES

- Davis, David E. 1949. The role of intra-specific competition in game management. Trans. 14th N. Am. Wildlife Conf.: 225-231.
- Emlen, J. T., Jr., A. W. Stokes, and C. P. Winsor. 1948. The rate of recovery of decimated populations of brown rats in nature. *Ecology*, 29: 133-145.
- Emlen, John T., Jr., A. W. Stokes, and David E. Davis. 1949. Methods for estimating populations of brown rats in urban habitats. *Ecology*, 30: 430-442.

THE RELATION BETWEEN THE LEVEL OF POPULATION AND THE PREVALENCE OF LEPTOSPIRA, SALMONELLA, AND CAPILLARIA IN NORWAY RATS¹

DAVID E. DAVIS

*The Johns Hopkins University School of Hygiene and Public Health, Baltimore,
Maryland*

As a part of a study of the factors affecting the level of Norway rat (*Rattus norvegicus*) populations (Davis 1951a, 1951b) examinations for some of the internal parasites were made. Three well-known organisms were selected to serve as examples of the relationships of prevalence to population level. *Leptospira icterohaemorrhagiae* is a common spirochete that causes Weil's disease in man. *Salmonella* (several species) is a genus of bacteria known to be pathogenic to rats, humans, and many other vertebrates. *Capillaria hepatica* is a nematode that has a direct life cycle and is known normally only from rats.

The rats were caught in residential blocks in Baltimore in box traps and brought to the laboratory for examination. The size of the rat population in each block was estimated by the methods described by Emlen, Stokes, and Davis (1949). After a sample (usually half the rats) had been removed from a block with a stationary population, a second sample was taken a couple of months later from the now increasing population. In other blocks a decrease of population was due to a gradual deterioration of the environment (from the rat's viewpoint) rather than to trapping or poisoning.

The detection of *Leptospira* in the tis-

suess of the host was accomplished by direct microscopic examination, by animal inoculation, and by cultivation in an artificial medium. Both kidneys were removed aseptically from the animal and were ground with a mortar and pestle. A 30 per cent saline suspension of the finely divided tissue was centrifuged at 1,000 r.p.m. for 5 minutes to throw down the coarse particles, after which the supernatant fluid was examined under the dark-field microscope for the presence of spirochetes. One and one-half to two ml. quantities of suspensions from specimens in which no *Leptospira* could be demonstrated microscopically were injected intraperitoneally into young guinea pigs, which were examined daily thereafter for evidence of infection. Microscopically negative suspensions were also inoculated into Schüffner's medium and incubated at 30° C. for a period of three weeks, during which time periodic microscopic examinations were made. In some instances, the presence of *Leptospira* was demonstrated by this method when other methods failed. Serological identification of every fifth positive culture showed *Leptospira icterohaemorrhagiae* to be the species present in every case.

Examinations for *Salmonella* were conducted simultaneously with those for *Leptospira*. Suspensions of liver, kidneys, and caecal contents were pooled with urine removed from the bladder and streaked directly upon SS Agar plates. The same specimens were inoculated into Tetrathionate Broth, an enrichment medium, which was streaked upon SS Agar plates after an incubation period of 24 hours at 37° C. Final identification of organisms producing characteristic colonies upon SS

¹ Contribution from the Vertebrate Ecology Division of the Department of Parasitology, The Johns Hopkins University School of Hygiene and Public Health. This investigation was supported in part by a research grant from the Division of Research Grants and Fellowships of the National Institutes of Health, U. S. Public Health Service. The bacteriological examinations were done in the laboratories of the Department of Bacteriology of the Johns Hopkins University School of Hygiene and Public Health.

TABLE I. *Prevalence of Leptospira according to population level*

Population	Males		Females		Total	
	Rats	% pos.	Rats	% pos.	Rats	% pos.*
Stationary	271	47.2	272	43.4	543	45.3
Increasing	165	52.3	161	47.9	326	49.9
Decreasing	143	52.4	164	45.6	307	48.9
Total	593	49.7	624	44.2	1217	46.9

* See text for definition of positive.

Agar was made by biochemical and serological methods.

The examination for *Capillaria* consisted of noting macroscopically the presence or absence of the characteristic lesions in the liver.

The results for *Leptospira* (Table I) show no significant difference among the three categories of blocks. While additional data might reveal a significance for the difference ($P = \text{only } 0.17$) between stationary and increasing populations, the difference would be slight. These are crude prevalences but analysis by consideration of the differences related to weight or length (Table II) does not indicate any differences among the three categories of populations. Apparently the frequency of contact was not sufficiently lowered by removal of rats to affect the transmission in the blocks that contained sub-asymptomatic populations. It would be expected that these increasing populations would have a lower prevalence.

TABLE III. *Presence of Salmonella in blocks*

Block	Rats examined	Rats positive
A	69	4
B	38	1
C	11	5
D	10	3
E	10	3
F	16	2
G	15	1
H	29	11
I	65	4
J	63	2
K	21	2
L	20	1
		39

The evidence may also be interpreted to indicate that *Leptospira* has little, if any, pathogenicity for weaned rats. Other evidence results from an analysis of the ratio of weight to length for rats that were positive or negative for *Leptospira*. These ratios were the same. The absence of a difference between the two groups is interpreted to mean that the infection does not cause the rat to lose weight (or to fail to gain).

Salmonella was rare in all populations. It was present in only 4.0 per cent of 974 rats from the blocks, and hence no analysis of relation to population level is possible because of the small numbers. The 39 *Salmonella* infections were found in a total of 12 out of 37 blocks. Table III gives the details concerning the number of rats examined from each block and the number positive. The proportions are

TABLE II. *Relation of size of rat to prevalence of Leptospira*

Weight	Males		Females		Length	Males		Females	
	Rats	% pos.	Rats	% pos.		Rats	% pos.	Rats	% pos.
0-99 g	62	14.5	71	14.1	80-99 mm	1	100	0	—
100-199	88	21.6	99	18.1	100-119	11	18.2	15	13.3
200-299	82	54.8	113	38.6	120-139	28	17.8	26	19.3
300-399	150	60.0	171	58.5	140-159	34	14.7	42	11.9
400-499	147	61.2	134	60.5	160-179	50	22.0	59	20.3
500-599	62	66.2	33	69.6	180-199	44	23.8	41	21.9
600-699	2	50.0	1	0	200-219	102	55.0	123	45.5
					220-239	203	60.6	191	57.6
					240-259	104	63.4	113	66.3
					260-279	7	85.6	2	0

TABLE IV. *Prevalence of Capillaria according to population level*

Population	Males		Females		Total		Male and female			
							0-199		200-599	
	Rats	% pos.	Rats	% pos.	Rats	% pos.	Rats	% pos.	Rats	% pos.
Stationary	358	96.5	352	95.3	710	95.5	239	86.2	887	96.9
Increasing	204	96.5	202	94.5	406	95.5				
Decreasing	169	91.8	175	87.8	344	89.8				
Total	731	95.2	729	93.3	1460	94.1	87	68.9	257	97.0
Comparison							Significance (P)			
Stationary-Decreasing							0.0005			
Increase-Decrease							0.0027			
0-199 g and } 200-599 g rats }							0.007			

fairly high in some blocks. The population of rats in the block from which 11 positive rats were obtained had declined during the artificial introduction of rats from about 96 rats to 72 rats and then had increased to 94 rats when the sample was captured. If an epidemic was started by the introduction of rats carrying *Salmonella* and was responsible for the large number of positive rats, there was no observable effect on the number of rats in the block as indicated by the increase of rats to 94. It may be remarked that a similar history of decrease during introduction of rats, and of increase after cessation of the introductions, occurred in a population from which no *Salmonella* were isolated.

The prevalence of *Capillaria* is very high in the rats from the city blocks (Table IV). The prevalence is significantly

lower in the decreasing populations than in the stationary or the increasing populations. A comparison according to size groups (Table IV) shows that large rats in the stationary and the decreasing populations have the same prevalence and that the difference lies in the small (0-199g.) rats. A mechanism to account for this difference is not apparent. One would expect that young rats would pick up the eggs as readily in a decreasing population as in any other. However, it should not be concluded that the blocks with decreasing populations have more deaths of large rats (hence heavily infested with *Capillaria*) than other blocks because the decreases were apparently due to infant mortality rather than to adult mortality.

The relation of weight and length to prevalence of *Capillaria* is shown in Table

TABLE V. *Relation of size of rat to prevalence of Capillaria hepatica*

Weight	Males		Females		Length	Males		Females	
	Rats	% pos.	Rats	% pos.		Rats	% pos.	Rats	% pos.
0-99 g	46	58.7	63	63.5	80-99 mm	1	0	2	0
100-199	119	95.6	117	83.9	100-119	8	37.5	10	60.0
200-299	126	94.4	154	96.7	120-139	20	54.9	20	85.0
300-399	197	97.8	226	97.1	140-159	47	87.2	46	84.7
400-499	192	98.3	178	99.3	160-179	66	98.5	72	82.0
500-599	83	98.8	46	100	180-199	69	92.7	67	94.0
600-649	5	100	1	100	200-219	151	96.6	166	97.6
					220-239	273	97.6	259	98.8
					240-259	125	99.2	126	99.0
					260-279	9	100	2	100

V. It is noteworthy that many of the young rats are infected by the time they leave the parental nest as shown by the large number of infections in rats measuring 80–199 mm in length.

SUMMARY

To determine the relation of pathogenic organisms to the level of rat (*Rattus norvegicus*) populations, examinations of rats from known populations were made to determine the prevalence of *Leptospira icterohaemorrhagiae*, *Salmonella* spp. and the nematode *Capillaria hepatica*.

The results of the examinations for *Leptospira* showed no difference in prevalence in blocks with stationary, increasing, or decreasing populations. The prevalence increases with the size of the rat. *Salmonella* was found in only 4.0 per cent

of 974 rats but 2 blocks had a high proportion of positive rats. *Capillaria* was significantly less prevalent in blocks with decreasing populations than in blocks with stationary or increasing populations. The prevalence was 94.1 per cent in the city blocks.

It is concluded that the available evidence does not indicate that these three organisms have a measurable effect on population level.

REFERENCES

- Davis, David E. 1951a. The relation between level of population and pregnancy of Norway rats. *Ecology*, 32: 459–461.
- Davis, David E. 1951b. The relation between level of population and size and sex of Norway rats. *Ecology*, 32: 462–464.
- Emlen, John T., A. W. Stokes, and David E. Davis. 1949. Methods for estimating populations of brown rats in urban habitats. *Ecology*, 30: 430–442.

A COMPARISON OF REPRODUCTIVE POTENTIAL OF TWO RAT POPULATIONS¹

DAVID E. DAVIS

The Johns Hopkins University School of Hygiene and Public Health, Baltimore, Maryland

A previous study (Davis 1949) showed that the striking differences in size between Norway rats (*Rattus norvegicus*) living in the residential areas of Baltimore and rats living on a farm near Baltimore were largely phenotypical. Laboratory experiments proved that rats from both populations grew at the same rate and attained the same size when they were raised on the same diet. At that time, data on certain growth and reproductive characteristics were not available for the farm rats. Hence it is the purpose of this paper to compare certain growth and reproductive characteristics of the two populations. Such comparative studies of the productivity of mammalian populations are rare. Morton and Cheatum (1946) compared the reproduction of deer in northern and southern New York State. Most other studies of reproduction refer only to one population and hence are not comparative. Obviously an analysis of reproductive rates is fundamental to an understanding of population changes, dispersal, and mortality rates.

The rats were captured during two years from June, 1947 to June, 1949. The city rats were obtained by trapping in residential areas of Baltimore. There the rats lived in yards, basements, and garages and fed upon garbage. The farm rats were captured on a horse-breeding farm about 16 miles north of

Baltimore. There the rats lived under the buildings, in the stalls, and between the double walls of the horse barns and cow barn. They ate horse feed, manure, and an occasional dead rat or fowl. This is the deficient diet.

The city rats came from stationary, increasing, or decreasing populations. These changes reflected environmental changes as well as the result of reductions from trapping. Seasonal population changes due to seasonal differences in the reproductive rate are not detectable with present census methods. The farm population during the first year averaged about 300 rats. The changes were due both to local changes in the environment and to seasonal changes in reproduction. During the second year the population increased to about 600.

After capture, the rats were autopsied in the laboratory, and the data recorded on punch cards. The numerical totals in the tables do not all agree because data for a characteristic may be lacking. For example in Table I the weights of 402 male farm rats were recorded but the lengths of only 390; the unrecorded ones were due to inability to measure the rat for some reason. These differences are small and are random and hence do not introduce any systematic error. The city rats here described are not the same rats analyzed in the previous paper (Davis 1949).

COMPARISON OF SIZE AND GROWTH

The mean length and mean weight for males and for females is given in Table I. Significant differences ($P < 0.002$) exist for both weight and length between farm and city rats. There is no difference in size of male and female farm

¹Contribution from the Division of Vertebrate Ecology of the Department of Parasitology, The Johns Hopkins University School of Hygiene and Public Health. The work reported in this paper was conducted under a grant from the International Health Division of the Rockefeller Foundation, and a grant from the National Institutes of Health, U. S. Public Health Service.

TABLE I. *Comparison of size of farm and city rats*

	Farm		City	
	Male	Female	Male	Female
Total rats	390	387	1102	1132
Mean length (mm)*	171.7	168.9	203.7	200.1
Standard deviation	30.6	32.6	39.6	41.8
Total rats	402	392	1109	1150
Mean weight (g)	169.9	167.3	320.7	288.1
Standard deviation	105.2	77.8	154.3	132.6

* Length of head plus body.

rats but the male city rats were heavier ($P < 0.05$) but not longer than the female city rats.

The relation between length and weight (Table II) shows that the rats gain weight at the same rate proportional to length but that the city rats attain a much greater size. It is interesting to note that the reduced rate of gain of the females begins at about 205 mm for farm rats and at about 235 mm for the city rats. This suggests that farm rats of 205 mm are equivalent to city rats of 235 mm in this aspect of growth.

A comparison of the size at which 50 per cent of the rats attain a given char-

acter is useful for comparison of two populations. Table III presents the 50 per cent points for five different characters. The eruption of the third molar tooth can readily be determined by forcing the mouth wide open to see if the gums cover this tooth. Ossification of the skull refers to the extent of bone formation as determined qualitatively by resistance to pressure by the fingers. Descent of testis refers to the presence of testes in the scrotum. Perforation of vagina refers to the opening of the vaginal orifice by rupture of the membrane. Presence of placental scars refers to the appearance of dark spots on the mesometrial side of the uterus, resulting from implantation of the placenta. It is recognized that these measures are rather crude but they are sufficient for the present purpose.

From Table III it is obvious that the farm rats attain these characteristics at essentially the same size as do the city rats. The only significant differences are for the weight at descent of testis and for the weight at perforation of vagina.

TABLE II. *Mean weight and standard deviation (S.D.) in grams, as a function of length*

Midpoint length*	Farm Male			Farm Female			City Male			City Female		
	Rats	Mean weight	S.D.	Rats	Mean weight	S.D.	Rats	Mean weight	S.D.	Rats	Mean weight	S.D.
85	0	—	—	1	25.0	—	3	25.0	—	0	—	—
95	2	35.0	—	1	35.0	—	1	35.0	—	5	25.0	—
105	9	46.1	—	9	39.5	—	8	41.5	—	17	44.4	9.4
115	23	46.3	0.5	20	52.5	8.9	23	48.0	3.1	29	48.4	8.0
125	29	61.9	7.4	34	63.7	8.5	35	62.1	12.6	44	61.8	8.5
135	25	76.6	10.0	25	77.4	9.4	39	74.7	11.7	38	70.5	10.7
145	28	91.4	14.7	31	86.6	12.7	51	92.6	11.8	54	90.5	15.2
155	31	113.4	9.9	21	110.2	15.9	36	116.4	15.0	36	113.3	17.3
165	31	145.0	40.0	33	136.2	19.4	44	137.0	20.0	51	135.4	16.5
175	31	173.7	30.4	42	172.4	27.8	41	158.7	18.0	59	166.4	26.6
185	39	204.8	35.1	41	199.6	29.6	43	206.3	31.2	40	200.0	25.3
195	53	246.1	42.4	43	229.4	41.6	63	237.1	36.3	58	242.7	35.2
205	35	286.7	40.8	39	263.7	45.7	78	280.4	39.4	96	272.8	43.9
215	28	330.0	44.4	29	298.8	43.0	133	331.2	44.7	131	325.9	41.8
225	20	370.5	35.2	10	322.0	52.6	173	384.5	61.1	157	393.2	53.9
235	5	422.5	—	2	345.0	—	172	431.1	50.2	159	423.3	58.9
245	0	—	—	0	—	—	100	486.2	46.2	116	462.2	53.4
255	0	—	—	0	—	—	46	531.3	52.5	42	496.7	56.9
265	0	—	—	0	—	—	8	556.2	—	1	545.0	—
275	0	—	—	0	—	—	1	605.0	—	1	605.0	—

* Length of head plus body in mm.

TABLE III. *Comparison of 50 per cent points for growth characters*

		Male		Female	
		Farm	City	Farm	City
Eruption of third molar	Weight (g) Length (mm)	54 115	51 119	55 123	48 116
Ossification of skull	Weight (g) Length (mm)	79 131	88 144	80 127	91 144
Descent of testes	Weight (g) Length (mm)	157 165	109 155		
Perforation of vagina	Weight (g) Length (mm)			72 134	123 150
Presence of placental scars	Weight (g) Length (mm)			— —	305 212

TABLE IV. *Comparison of pregnancy and of lactation*

Midpoint length (mm)	City		Farm		Midpoint weight (g)	City		Farm	
	Females	Per cent	Females	Per cent		Females	Per cent	Females	Per cent
Pregnancy									
155	22	0	20	0	75	60	0	73	0
165	44	0	33	3.1	125	78	0	57	3.5
175	53	3.8	48	25.0	175	75	6.7	74	20.3
185	40	7.5	41	19.5	225	79	16.5	66	28.7
195	60	21.6	43	30.3	275	115	20.9	34	17.6
205	94	27.7	39	28.2	325	132	22.7	23	48.0
215	130	23.1	28	35.7	375	146	26.7	11	54.5
225	155	28.4	11	36.4	425	120	31.7	0	—
235	157	31.8	2	0	475	107	32.7	0	—
245	113	32.8	0	—	525	50	46.0	0	—
255	36	25.0	0	—	575	15	66.7	0	—
265	1	0	0	—	Totals	917	23.4	265	22.2
275	1	100.0							
Totals	884	24.4	245	24.1					
Lactation									
165	51	0	33	0	125	110	0	58	0
175	59	0	47	2.1	175	81	3.7	74	17.6
185	40	7.5	41	19.5	225	80	18.8	66	30.3
195	60	26.7	43	44.2	275	117	29.1	34	50.0
205	95	32.7	39	43.6	325	132	54.5	26	50.0
215	131	51.9	29	62.0	375	148	56.7	12	41.7
225	156	62.1	11	36.4	425	123	65.1	0	—
235	159	54.6	2	50.0	475	110	61.0	0	—
245	116	60.4	0	—	525	53	58.5	0	—
255	36	58.3	0	—	575	16	68.7	0	—
265	1	0	0	—	Totals	860	46.2	212	32.1
275	1	100							
Totals	854	46.4	212	32.1					

However, the 50 per cent points cannot be compared directly because the farm rats are smaller than the city rats. The significances must be calculated for the ratio of the 50 per cent point to the mean size of the population. These calculations are not presented here in detail but show that the farm rats attain these characters at significantly ($P < .05$) larger relative sizes for all characteristics' except weight at perforation of vagina and length at ossification of skull for females. It thus seems established that the farm rats grow more slowly and attain most of these physiological characters at a relatively larger size. In passing it should be noted that the farm rats never attained even 50 per cent presence of placental scars and hence the points could not be calculated.

On the farm 50.0 per cent of 781 rats were males; in the city 49.4 per cent of 2250 rats were males. Obviously the percentages do not differ from each other or from 50 per cent.

COMPARISON OF REPRODUCTION

The relations between length or weight and prevalence of pregnancy or of lacta-

tion are given in Table IV. A rat was classed as pregnant if the embryos were macroscopically visible and thus gives about 18/22 of true pregnancy. A rat was classed as lactating if milk could be expressed by one's fingers from the nipples. In all cases the prevalences increase with size in a similar manner although the slope of the increase is somewhat greater in farm rats as would be expected because of their smaller size.

Seasonal changes in pregnancy and lactation also occur (Table V). Pregnancy was determined by visibility of embryos in the uterus and hence does not include rats with unimplanted blastocysts. The percentages are comparable because the same method was used at all seasons and are about 18/22 of the total pregnancies. For present purposes the adult female populations are defined in two different ways. Rats with a perforate vagina include all that possibly could conceive young. Rats with 10-12 visible nipples are larger and usually (80 per cent) have already conceived. The seasons were determined by examination of a hythergraph which shows the relation of temperature and precipitation by

TABLE V. *Seasonal changes of pregnancy and lactation*

	Seasons								
	Hiber- nal	Prever- nal	Vernal	Estival	Post- estival	Sero- tinal	Autum- nal	Total	Stand- ardized percent- ages
Pregnancy									
Farm rats with perforate vagina	115	40	43	27	1	60	26	312	—
Per cent pregnant	11.3	45.0	20.9	25.9	0	20.0	3.8	19.2	21.1
Farm rats with 10-12 nipples	65	26	23	22	0	33	8	178	—
Per cent pregnant	16.9	61.5	39.1	40.8	—	27.2	12.5	30.9	33.0
City rats with perforate vagina	272	129	199	101	62	98	54	915	—
Per cent pregnant	19.5	22.5	28.6	27.7	22.6	21.5	27.8	23.7	24.6
City rats with 10-12 nipples	248	110	166	85	52	83	44	787	—
Per cent pregnant	21.4	26.3	33.1	31.2	26.9	25.3	34.2	27.4	28.4
Lactation									
Farm rats with perforate vagina	115	40	43	22	1	60	26	307	—
Per cent lactating	20.0	37.5	32.6	22.8	0	18.3	0	22.2	22.0
Farm rats with 10-12 nipples	66	27	23	22	0	33	8	179	—
Per cent lactating	34.9	55.6	61.0	22.7	—	33.3	0	38.0	34.6
City rats with perforate vagina	274	129	199	101	62	99	54	918	—
Per cent lactating	31.1	45.7	60.2	44.0	45.2	44.0	31.4	43.2	43.1
City rats with 10-12 nipples	249	110	167	85	52	84	44	790	—
Per cent lactating	30.1	53.7	71.9	51.8	53.9	52.4	63.0	50.3	53.9

TABLE VI. *Comparison of number of embryos*

Midpoint length (mm)	City		Farm		Midpoint weight (g)	City		Farm	
	Females	Mean embryos	Females	Mean embryos		Females	Mean embryos	Females	Mean embryos
165	0	—	1	9.0	125	0	—	2	6.5
175	2	8.0	12	7.1	175	5	7.6	15	7.8
185	3	8.0	8	7.7	225	13	7.9	19	8.4
195	13	9.0	13	8.8	275	23	10.0	6	8.7
205	25	8.9	11	9.5	325	29	9.4	11	8.0
215	30	9.9	10	7.2	375	34	12.2	6	9.5
225	42	9.9	4	9.3	425	38	10.0		
235	51	10.8			475	35	10.8		
245	37	10.6			525	23	10.7		
255	9	11.4			575	9	12.0		
265	0	—							
275	1	9.0			Totals	209	10.4	59	8.2
Totals	213	10.1	59	8.2					

weeks. Homogeneous groups of weeks were delimited and called seasons. From Table V it will be noted that the farm rats have a sharp increase in pregnancy in the prevernal (roughly March–April) and a probable increase in the serotinal (roughly September). The city rats had a peak in the vernal (roughly June) and estival (roughly July) and then in autumnal (roughly October) but none of these peaks is strikingly high. The percentage of lactation has about the same changes in both populations.

It is obvious from Tables IV and V that the city rats have a higher percentage of lactation ($P < 0.02$) but that the percentage of pregnancy is not significantly different from that of the farm rats. This difference will be mentioned further in a discussion of reproductive rate.

The number of embryos increases with length and with weight of the female (Table VI). The mean number of embryos is significantly larger ($P < 0.001$) in the city (mean = 10.1; S.E. = 0.188) than on the farm (mean = 8.2; S.E. = 0.309).

COMPARISON OF REPRODUCTIVE RATES

The preceding sections have described the relations of size of rat to percentage of pregnancy, of lactation, and to the number of embryos. Also the crude per-

centages by season and for both the farm and city are given. It is now proposed to use these data to attempt to contrast the reproductive rates of the two populations. It should be noted that we are dealing with crude prevalences. That is, we are comparing the actual reproduction of the two places; we are not comparing the reproduction as if both places had rats of the same size and age. Each method is valid for certain purposes; in this case our purpose is to contrast the number of young produced. The analysis of the reasons for the differences would require an examination of the size-specific prevalences.

The age at attainment of sexual maturity is apparently greater for farm rats than for city rats (Table III) if we assume that age is proportional to size. Thus rats from this farm would have a longer juvenile period before the first litter than do rats from the city. Unfortunately the data and methods at hand do not permit an evaluation of the extent of the difference.

From the data in Tables V and VI, a number of interpretative calculations are presented in Table VII. The annual incidence of pregnancy was calculated from $I_P = \frac{365P}{18}$ where I_P is incidence of pregnancy and P is prevalence of preg-

TABLE VII. *Incidence of pregnancy and lactation on farm and in city*

	Farm	City
Prevalence of pregnancy	.211	.246
Incidence of pregnancy	4.3	5.0
2 Standard errors	.0462	.0284
Upper limit	5.2	5.6
Lower limit	3.4	4.4
Prevalence of lactation	.220	.43
Incidence of lactation	2.2	4.3
2 Standard errors	.0296	.0328
Upper limit	2.5	4.8
Lower limit	1.9	4.2
Percentage loss of litter	49	10
Mean embryos per adult female	8.2	10.1
Young weaned (estimated)	13.6	35.0

nancy. The incidence of lactation was calculated from $I_L = \frac{365L}{36}$ where I_L is incidence of lactation and L is prevalence of lactation. The figure 365 represents the number of days in the year and 18 and 36 represent the number of days during which pregnancy or lactation, respectively, can be determined by the methods used here. The limits for both incidences were calculated by adding and subtracting 2 standard errors ($S.E. = \sqrt{pq/n}$) to the prevalences and then calculating the corresponding incidences. The prevalences are standardized in Table V for seasonal changes so that the data may be compared. The standardization was done merely by obtaining the mean of the percentages for each season, thereby in effect assuming that 100 rats were caught in each season. Strictly the standard error should be calculated from

$$S.E. = \frac{1}{4} \sqrt{\sum (S.E. \text{ for each season})^2}.$$

From a comparison of the limits in Table VII it can be seen that the limits for the incidences of pregnancy overlap. However, the incidences of lactation do not overlap even at a level of $P = 0.001$. Hence it seems safe to conclude that the farm females on the average have the same number of pregnancies but suckle fewer litters than do the city females.

From the comparison of pregnancies and lactations it is clear that the loss of entire litters between pregnancy and lactation was greater on the farm (49.0 per cent) than in the city (10.0 per cent). It must be noted that these methods do not tell how many litters are born nor how many are weaned. The calculated losses are really between the fifteenth day of pregnancy and the eighteenth day of lactation.

While we can conclude that the city rats suckle about twice as many litters as do the farm rats, we must make some assumptions to translate these values into the number of young weaned. We know that the pregnant females from the farm average 8.2 embryos and from the city 10.1 embryos. We do not know how many individuals are born nor how many are lost at parturition, and during suckling. But if we assume that the loss is about 2 young per litter at and after parturition and also assume that the number of litters being suckled (prevalence of lactation) is practically the same as the number of litters weaned, then the farm rats weaned 13.6 young (6.2×2.2) and the city rats weaned 35.0 young (8.1×4.3). This is the average annual production for an adult female (one with a perforate vagina).

It may be worth while to speculate about the death rate. On the farm the population increased from about 300 to about 600 rats during the year. Since about 40 per cent of the rats were breeding females there was an average of $450 \times 0.4 = 180$ breeding females (assuming a linear increase) and $180 \times 14 = 2520$ young rats weaned. The death rate then is $2520/450 = 5.6$ deaths per rat per year. This means that during the year almost 6 times the average population died. By the same reasoning the death rates of the city populations can be calculated. Most of these populations were stationary in numbers. If we assume a stationary population then $0.4 \times 35 = 14.0$ is the death rate.

These values must not be taken lit-

erally because of the assumptions and estimations in the computations. The rates however do indicate how great differences in birth rates may be compensated for by differences in death rates. The farm population had low birth and death rates but increased. The city population in these blocks had high birth and death rates but remained nearly stationary.

SUMMARY

The discovery that the reason Norway rats (*Rattus norvegicus*) living in the city were significantly larger than rats on a farm was a deficient diet on the farm suggested a comparison of the growth and reproductive rates. Hence a comparison of size at attainment of several growth characters and a comparison of production of young was made. It was found that city rats grew larger and attained reproductive maturity at a smaller size than did the farm rats.

Pregnancy was correlated positively with size in both populations. The crude

incidence of pregnancy was not significantly different in the two places but the incidence of lactation was significantly higher in the city (4.3 per year) than on the farm (2.2 per year). Also the mean number of embryos was significantly higher in the city (10.1) than on the farm (8.2). Allowing for a 20 per cent mortality at and after birth, the city females weaned about $8.1 \times 4.3 = 35.0$ young per year while the farm females weaned about $6.2 \times 2.2 = 13.6$ young.

Using these values and a knowledge of population changes it is estimated that the death rate in the city was about 14.0 and on the farm was about 5.6 deaths per rat per year.

REFERENCES

- Morton, Glenn H., and E. L. Cheatum. 1946. Regional differences in breeding potential of white-tailed deer in New York. *J. Wildlife Manag.*, 10: 242-248.
- Davis, David E. 1949. A phenotypical difference in growth of wild rats. *Growth*, 13: 1-6.

AN UPLAND FOREST CONTINUUM IN THE PRAIRIE-FOREST BORDER REGION OF WISCONSIN¹

J. T. CURTIS

University of Wisconsin, Madison

and

R. P. MCINTOSH

Middlebury College, Middlebury, Vermont

INTRODUCTION

It has been said that the desirable order of ecological research in a given region is first, the study of communities, second, the study of the individual species, and last, the study of the habitat (Yapp 1922). Sociological investigations of constituent species and their numerical relations should precede autecological studies if the latter are to have maximum meaning. This sequence should lead to a greater efficiency in research, in that an initial knowledge of any natural groupings of species may enable the autecology of the groups to be studied simultaneously, with a resultant saving in time and travel expenses. The grossly inadequate state of autecological knowledge of even our most common species indicates that the current haphazard method of attack is faulty; if aggregations of species occur together under similar environmental conditions in nature, they could be studied in a systematic program. A long-term investigation of the communities of Wisconsin has been underway since 1946 with a view to determining the existence and the floristic nature of such aggregations (Curtis and Greene 1949). The present paper deals with the upland hardwood forests of the prairie-forest border region of the state and their interrelations with each other and with certain physical factors of the environment. Deep appreciation is expressed to Professor P. B. Whitford, who

generously placed his files on forest composition at our disposal; to Professors Grant Cottam, H. C. Greene, N. C. Fassett, R. S. Muckenhirn, M. L. Partch, and S. A. Wilde for valued advice and consultation; to Messrs. Orlin Anderson, and R. S. Brown for indispensable aid in the collection of field data; to Miss Margaret Gilbert for aid in the computation; to Messrs. A. M. Fuller, Neil Harrington and Fred Wilson for help in the location of stands; and to the many members of the Soil Conservation Service, the Regional Foresters of the Wisconsin Conservation Department and the advisers of the Junior Wisconsin Academy of Sciences, who so willingly imparted their knowledge of local conditions in their regions. The authors are also indebted to Professor K. J. Arnold, of the University Computing Service, for aid in the statistical phases of the work.

The taxonomic nomenclature used in this paper follows that of Gray's *Manual of Botany*, 8th edition, 1950.

LITERATURE REVIEW

The earliest references to the vegetation of southwestern Wisconsin were made by the explorers and pioneer travelers in the years following 1698. For the most part, they contained only general descriptions, with remarks about unusual species. The first account by a competent botanist was that of Increase A. Lapham in 1852, but he dealt primarily with the distribution of individual species. The first description of plant communities as such was given by T. C. Chamberlain in 1877. This eminent geologist, who was later to exert such great

¹This work was supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation.

influence on H. C. Cowles at the University of Chicago, was at that time the State Geologist of Wisconsin. He distinguished three forest communities in southern Wisconsin, but made clear that no abrupt line of demarcation existed between them, with repeated statements illustrating "a gradual transition from one to the other" and "an almost imperceptible merging of one into the other." His three communities were the "oak group" including *Quercus alba* (white oak), *Q. macrocarpa* (bur oak), *Q. rubra* (red oak), and *Q. velutina* (black oak), with *Populus tremuloides* (aspen), *Carya ovata* (shagbark hickory), *Prunus serotina* (black cherry) and *Pyrus ioensis* (wild crab apple) as lesser members; the "oak and maple group" in which *Acer saccharum* (sugar maple) was most conspicuous but *Quercus alba* and *Q. rubra* were still common, with *Acer rubrum* (red maple), *Ulmus rubra* (slippery elm), and *Tilia americana* (basswood) in small numbers; and the "maple group" with *A. saccharum* dominant, but with *Tilia americana*, *Ulmus rubra*, and *Ostrya virginiana* (ironwood) as characteristic and abundant associates. He comments about the "oak and maple group" as follows: "This group is not characterized by the exclusive presence of any prominent plant but by a distinctive association of plants common to several groups."

Bruncken (1900) also described three forest associations, but only two were found on uplands—the "hemi-xerophytic oak-hickory" and the "mesophytic basswood-maple." Additional observational studies on the forests of the region were reported by Pammel (1904), Marks (1942) and Stout (1944), but the first account in which quantitative data on actual composition were presented was that of Wagner (1947), who studied a stand in Jefferson County which fits into Chamberlain's oak and maple group. Cottam (1949) investigated an oak woods in Dane County by quantitative methods and reported in detail on the historical development of oak openings

and the changes which have taken place in them since settlement. He attributed major importance to fire in the maintenance of oak openings and to cessation of fire as the cause of the subsequent development of the present closed canopied stands.

The most comprehensive paper on the forests of southern Wisconsin was by Whitford (1951). Although this study was primarily concerned with the relation between the clone size of herbs and the age of the forest stands, considerable attention was devoted to the establishment of a method for classifying the stands. In the course of the investigation, Whitford studied a considerable number of stands and presented detailed data on tree, shrub, and herb composition. He arranged his series of 28 stands into three groups on the basis of shade tolerance of the tree species. He assigned each species to one of three tolerance classes, and then determined the relative fraction of all trees in a stand which belonged to each of these classes, on a summation basis. This method resulted in a sequence of stands from those composed entirely of intolerant species to those made up mostly of tolerant species. Whitford divided his stands into three groups—"oak-hickory, intermediate, and maple-basswood," but the division was made for pragmatic reasons and was not based on any internally apparent separation of the data into three groups.

Studies in Illinois, Iowa and Minnesota indicate that a series of forests similar to those in Wisconsin are found in at least portions of these states. No quantitative investigations in northern Illinois have come to our attention, but the general descriptions of Fuller and Strassbaugh (1919), and DeForest (1921) indicate a series of forest types from those dominated by *Quercus* and *Carya* to those dominated by *Acer saccharum*. In Iowa, the studies of Clark (1926) and of Aikman and Smelser (1938) show a succession from *Quercus macrocarpa* and *Q. velutina* in the initial stages through

Quercus rubra-*Tilia americana* stands to the terminal forests of *Acer saccharum* and *Tilia americana*. Daubenmire (1936) reported on the structure of the *Acer-Tilia* community and on its relation to the surrounding *Quercus* forests in the "Big Woods" of Minnesota.

While the results of the various investigations in these four states are by no means in complete agreement, there does appear to be a general uniformity of opinion as to the topographic distribution of the forests, with some type of *Quercus* forest on the most xeric forested sites and an *Acer* forest in the most mesic habitats. The disagreement seems to lie in the determination of the number of discrete communities that may be recognized, in the floristic nature of the boundaries between them, and in their exact composition. Many of the early workers emphasized the lack of sharp lines of demarcation, while later workers, who could study only the more completely dissected and isolated stands resulting from the highly agricultural land use of the present time, were more inclined to describe discrete communities of several types.

Although the flora of Wisconsin has many diverse floral elements, it was early pointed out that there are two major floristic provinces, separated by a diagonal line from northwest to southeast (Cheney 1894). The southwestern portion of the state contains the prairies and hardwood forests, while the northeastern part contains both hardwood and coniferous forests. The boundary line between them; actually a zone or band, is comparable to the tension zone proposed by Griggs (1914). Its position can be determined within fairly narrow limits by the method proposed by Clements (1905: 187) "The limiting line or ecotone of a . . . province is a composite obtained from the limits of principal species and checked by the limits of species typical of the contiguous vegetations."

Applying this to Wisconsin, a number of trees including *Quercus velutina*,

Carya ovata, and *Juglans nigra* reach their northern boundaries in a zone which also includes the southern limits of such trees as *Betula lutea*, *Abies balsamea*, and *Populus balsamifera*. This same zone marks the northward or southward extent of a great many herbaceous species, both native and exotic; it also separates closely related varieties of single species, as in the case of *Acer saccharum saccharum* and its subspecies *A. s. nigrum* (Desmarais 1948) and *Brachyelytrum erectum erectum* and *B. e. septentrionale* (Salamun 1950). The floristic province southwest of the zone is here termed the prairie-forest province, while that to the northeast is the northern hardwoods province (roughly equivalent to the Lake Forest of Weaver and Clements 1938). It is recognized that these names may be of local descriptive value only and are considered to be tentative. Perhaps the most characteristic feature of the floristic provinces from the standpoint of vegetation is the occurrence of oak woods in the early forest succession south of the zone in contrast to pine woods in the same successional position north of the zone. The terminal forests in both provinces are dominated by sugar maple. Within the narrow zone itself various elements of the two provinces occur in puzzling mixtures. Their elucidation must await completion of studies on both sides of the zone.

These floristic provinces are similar to the natural areas of Cain (1947) and the floristic areas of Raup (1947) and Egler (1948). They are characterized by the presence of a uniform flora such that "all stands have equal chances of containing all the same species" (Cain 1947). It is only within such limitations that plant associations can possibly achieve objective reality. One of the aims of the present paper is to determine whether discrete communities with definite structure and definable boundaries actually exist within such a natural floristic province, or whether plant associations are "metaphysical approximations

in a field where there are unlimited variables, combinations and permutations" (Cain 1947) even within the narrow limits set by the province.

DESCRIPTION OF AREA

Physiography

The south and west borders of the area included in this study (the Wisconsin-Illinois boundary and the Mississippi River) were prescribed by various non-ecological but nevertheless compelling reasons. The remaining boundary was based on the biologically more valid presence of the tension zone discussed above which extends across Wisconsin from northwest to southeast (Fig. 1). The major physiographic differentiation of the region is its separation into glaciated and non-glaciated areas. The Driftless Area in the western portion of the study area is a region of mature drainage patterns and rugged, almost mountainous, topography as contrasted with the glaciated eastern portion which possesses immature drainage and a more or less rolling topography. The glaciated areas consisted primarily of Wisconsin drift with lesser areas of older (Illinoian)

drift. The underlying bedrock is composed predominantly of old sedimentary rocks—Cambrian sandstones and Lower Magnesian, Ordovician and Silurian limestones.

Climate

The area under consideration lies almost wholly in the transition zone between climatic regions I and IV of Borchert (1950). As such, its climate is intermediate between that of the Northeastern forest region of snowy winters and reliable summer rains and that of the central Prairie region with relatively dry winters and frequent summer droughts. Partaking of both forest and grassland climates, it supports both prairie and forest and their intermediate expression, the oak savanna. Excellent summaries of the ecologically significant climatic variables for the general region are mapped by Borchert (1950).

Soil

The forest soils of the area belong to the grey-brown podzolic soil group and are largely of the Fayette-Dubuque series in the Driftless Area and the Miami-Bellefontaine series in the eastern glaciated area. The topsoils in both series are usually composed of loess or a mixture of loess and residual soil. Profile characteristics are similar throughout the study area. In general, there is a well-marked dark A_1 layer varying from one-half inch to as many as ten inches in depth, although one to four inches is more typical. The A_2 is not well defined in terms of color but may be detected by textural differences; it is usually one-half to two inches in depth. The brownish B layer generally shows a well-defined nut structure.

General vegetation

The southwestern half of Wisconsin lies in the broad ecotonal belt between grassland and summergreen forest. In presettlement times its vegetation consisted of scattered prairies, oak openings

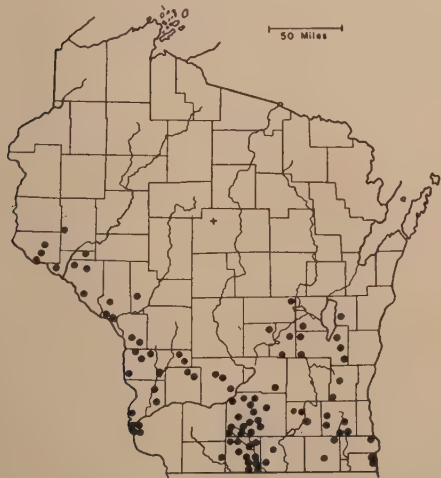


FIG. 1. Map of Wisconsin showing location of stands studied. The cross near the center of the map indicates 90° W. Long., 45° N. Lat.

of savanna-like aspect, and broadleaf deciduous forests of varying density and composition. The present-day stands of natural vegetation are mostly derived from these three communities, although other vegetation types are also present in the form of relics (McIntosh 1950). The deciduous forests occur on a range of topographic sites, from very dry through mesic to very wet. The driest sites, on cliffs, sandy soils and southwest slopes are characteristically covered with scattered stands of small oaks (*Quercus velutina*, *Q. macrocarpa*) or with red cedar (*Juniperus virginiana*) glades. As the moisture conditions improve, the forests become more dense, with a greater number of important tree species. The most mesic conditions commonly support sugar maple, basswood or other species of similar requirements. Wet soil forests are largely restricted to the flood plains of streams and rivers but are found to a limited extent also on the shores of glacial lakes in the eastern portion of the area. Their most characteristic trees are *Ulmus americana*, *Acer saccharinum*, *Fraxinus pennsylvanica lanceolata* and *Quercus bicolor*.

Most of the original prairie has been placed under cultivation but small remnants still occur along railroads and highways and occasionally elsewhere. Prairies of several sorts occurred on the same range of topographic types as the deciduous forests (Curtis and Greene 1949). Prairies formed a part of the presettlement vegetation of all counties included in the present study, although the area covered varied from less than one per cent in Richland County to over 50 per cent in LaFayette County. It is estimated that 20 per cent of the total area was in prairie when the first settlement by Europeans began in the 1830's.

METHODS

The plan of the investigation used in this work is an adaptation of the mass collection method used by taxonomists (Anderson 1941; Fassett 1941). It is

our conviction that variation in floristic composition is one of the most important characteristics that may be determined in the study of any vegetation, and this may be understood only after a great many examples of the type have been analyzed. It is important that the initial ideas of the type limits be sufficiently broad to preclude the dangers of subjective selection of only those stands which fit a preconceived notion as to what a particular community should be. The only criteria used for the selection of stands in the present study were: (1) that they be natural forests (*i.e.*, not artificially planted) of adequate size, fifteen acres being the minimum, with forty acres or more preferred; (2) that they be free from disturbances in the forms of fire, grazing or excessive cutting; (3) that they be on upland land forms on which run-off waters never accumulate. If a stand fulfilled these conditions, it was studied, regardless of what species of trees might be present. It might be expected that homogeneity would have been a required characteristic, but, as will be shown below, it was found that this could be determined statistically from the data at a later time. If a stand was then found not to be homogeneous, its data were eliminated from the compilations.

A few of the stands were known to us before the study was begun, but the majority were found in response to a circular letter sent out to state and federal forestry agencies, county agents, Soil Conservation Service personnel, and others whose work brings them into contact with woodlands. All of the stands discovered in this way were checked in the field, and, if they met the criteria of selection, they were incorporated in the study. In this way, an essentially random selection of 95 stands in 29 counties was obtained without prejudice as to kind. The geographical distribution of the samples (Fig. 1) was believed adequate to give an accurate picture of the forests of the area.

Field methods

Each stand was sampled by use of the random pairs method (Cottam and Curtis 1949). Forty pairs of trees were used for the determination of frequency, density and dominance. Presence was recorded for all vascular species on specially prepared forms which contained the names of the 200 plants most commonly found in upland forests of the region. Frequency of herbs, shrubs and tree seedlings was obtained by 20 quadrats, each $\frac{1}{4}$ milacre in size. Density was not determined for these forms.

Saplings over 1" DBH were counted in a transect between the two trees of each pair. Since the distance between the trees was variable, the transects resulted in different total areas in each stand and thus prevented the use of frequency as a measure. Density, therefore, is the only type of information available for the saplings. It appears desirable to devise some other methods of sampling saplings in future studies, for in many cases the sample derived by the method described above was inadequate.

As will be shown in detail elsewhere, the random pairs method, using 40 pairs of trees per stand, gives results whose accuracy compares very well with that obtained by the quadrat method. For example, a composite vegetational index (see below) by random pairs for three stands on which adequate quadrat data were also available showed an average deviation of only 2.9% from the index calculated from the quadrat figures. Duplicate analyses by the random pairs method made in three stands in two consecutive years by two sets of investigators showed an average trial to trial variation in the index of only 1.34%. This compares with an average deviation of 2.11% in five sets of quadrats made in as many years in one of the same stands. The random pairs method may therefore be assumed to give reproducible results of sufficient precision for the purposes at hand.

We knew of no way by which the homogeneity of stands could be determined objectively in the field, so it became necessary to devise a method of checking this after the data were collected. Since 40 separate pairs of trees are measured and recorded in sequence in the field, it is possible to segregate the data from successive groups of 10 pairs, each representing a different areal portion of the stand. Using these four groups as separate samples, the Chi-square test for homogeneity (Snedecor 1946) may be used to determine whether the actual occurrences of the major trees in any group deviate significantly from the occurrences expected on the basis of uniform distribution. The requirement of an expected value of at least five individuals in each sample makes this test applicable only to those tree species represented by at least 20 trees in 40 points. These species are the ones which determine the character of the stand in any case and if they are uniformly distributed, deviations on the part of lesser tree species are not likely to be significant. When this technique was applied to the current data it was found that in 95 cases only five Chi-square values exceeded the expected value at the five per cent level. In other words, five of 95 differed significantly from a homogeneous distribution. This approximates very closely the expected number (5 out of 100) of Chi-square figures which would exceed the expected by chance. On this basis it seemed reasonable to accept these as results of chance and reason for not rejecting the stands. This technique may be applied in the field in the future; if a stand is found not to be homogeneous further study will be in order.

Soil samples were collected separately from the A_0 , A_1 , and B horizons in most stands. This was accomplished by the use of three small pits located in representative portions of the wood, with the three subsamples pooled for later analysis.

Treatment of data

The data were tabulated and recorded on standard data sheets. Measures of number, size, and distribution for each tree species were calculated from the figures provided by the random pairs method for each stand. Relative (per cent) density and relative (per cent) dominance were determined in the ordinary manner, but frequency was calculated as percentage sum of frequency or relative frequency (Raunkiaer 1934, Curtis and McIntosh 1950), rather than the more usual simple frequency. The purpose of this change was to place frequency on the same mathematical basis as density and dominance, so that a summation index (density plus frequency plus dominance), with a constant value of 300 for all species in a stand could be prepared. The relative importance of a tree species is more clearly expressed by this method than by the DFD (density-frequency-dominance) index in its original form (Cottam 1948; Whitford 1949, Stearns 1951) where the sum was indeterminate. The index is calculated by adding the separate values of relative density, frequency and dominance for each species. Its magnitude is an excellent indication of the vegetational importance of a species within a stand, since it is sensitive to such variables as apparent contagion or exceptional basal area. This summation index of a particular species within a stand will be referred to herein as its *importance value* in order to differentiate it from the DFD index used by earlier workers. Not only does it differ because of its use of relative frequency, but because frequency as determined by the random pairs method is not strictly comparable to frequency measured by quadrat sampling. Quadrat frequency values bear a mathematical relationship to density values, with a fixed minimum ratio and a variable maximum depending chiefly on the degree of randomness or contagion exhibited by the species (Curtis and Mc-

Intosh 1950). Random pair frequency numbers, however, are more limited, in that they may range from equal to the density, down to one half the density, but they never can be smaller than one half the density values. As a result, frequency numbers usually are close to densities in absolute magnitude. The importance value, therefore, is weighted toward density, in that the number of trees present exerts a greater effect on the index than does their size. This seems proper in a floristic index.

Soil acidity and water-retaining capacity were determined in the laboratory on air-dried samples which were ground with a mortar and pestle and sieved through a 2 mm screen. Acidity was determined by the Helige-Truog method, while water-retaining capacity was measured by the Hilgard method. Analyses for available phosphorus, potassium, magnesium, and for organic matter were made by the Helige-Truog and Wilde methods at the State Soils Laboratory on the University campus. Exchangeable calcium was determined by volumetric analysis, also at the State Soils Laboratory. Nutrient ion concentrations are expressed as pounds per acre for the measured depth and weight of the particular horizon sampled. In the interests of brevity, only the data for the A_1 horizon are presented in this paper.

RESULTS

One of the difficulties inherent in the "mass collection" method of ecological study is the problem of handling the large quantities of diverse data that accumulate during the course of the investigation. It soon became apparent in the current work that the first requirement was a scheme for organizing or arranging the stands so that suitable comparisons of data could be made. To this end, an attempt was made to classify the stands into groups which had similar structure on the basis of tree composition. However, detailed examination of the data revealed no clear cut distinctions which

would readily separate the stands into such groups without the exercise of a considerable amount of subjective judgment.

It is possible to classify the stands objectively on the basis of the leading dominant trees in each. If the single leading dominant is used for this purpose it would be necessary to recognize 9 types in the 95 stands. The use of the first two tree species in order would necessitate recognizing 30 types; of the first three species, 75 types; of the first four, 95 types. In other words, no two stands of the 95 examined had the same arrangement of their first four most important tree species. The number of units recognized is thus determined entirely by the basis of selection and in no way represents an approximation of any natural groups. Accordingly, we attempted to devise a method whereby each species present in the stand might be taken into account in the classification of the stand. In this way, any tendency of the stands to fall into distinct groups would have maximum opportunity for expression.

A study of the importance values for all species soon showed that only a few species ever achieved high levels of importance. The majority of tree species never occurred as important elements in any of the stands. The ability of a tree species to achieve a given importance value, or what may be termed its importance potential, is the result of various hereditary physiological attributes whose nature is but poorly defined at present. Some species, like *Quercus alba*, reach major dominance in many forest stands covering a wide geographic area. Others, like *Gymnocladus dioica*, apparently never are important members of the forest community in any part of their range. Four tree species—*Quercus velutina*, *Q. alba*, *Q. rubra* and *Acer saccharum*—have an importance potential markedly greater than that of any other trees of southern Wisconsin (Table I). Since they are the major tree components

TABLE I. List of major tree species found in 95 upland hardwood stands of southern Wisconsin with data illustrating importance potential

Species	No. of stands of occurrence	Average importance value	Maximum importance value
<i>Quercus rubra</i>	80	90.4	228
<i>Acer saccharum</i>	45	82.8	201
<i>Quercus alba</i>	86	64.1	202
<i>Quercus velutina</i>	40	62.8	206
<i>Tilia americana</i>	63	39.6	179
<i>Ulmus rubra</i>	53	33.4	140
<i>Quercus macrocarpa</i>	25	24.8	170
<i>Fraxinus americana</i>	28	20.0	94
<i>Prunus serotina</i>	56	17.3	114
<i>Ostrya virginiana</i>	48	16.2	42
<i>Carya ovata</i>	39	15.7	61
<i>Acer rubrum</i>	18	13.3	58
<i>Juglans nigra</i>	21	12.5	30
<i>Carya cordiformis</i>	43	12.2	44
<i>Juglans cinerea</i>	23	12.1	53

of the upland forests of the region, it was decided to study their interrelations as a possible initial basis for community delimitation.

These four species were the leading dominants in 80 of the 95 stands studied. When these stands were placed in groups with the same leading dominant, it was found that seven stands had *Quercus velutina* as the major tree, 18 had *Q. alba*, 34 had *Q. rubra*, and 21 had *Acer saccharum*. The percentage occurrence (constancy, based on a sample of 80 trees in 40 random pairs) of each of the four species and their average importance values were calculated for each of these groups. The results are shown in Table II. The stands in which *Q. velutina* was the leading dominant had a greater average amount of *Q. alba* than of either of the other two tree species, and *Q. alba* was present in a much greater fraction of the stands. In stands dominated by *Acer saccharum*, *Q. rubra* was characteristically second in importance. On the other hand, stands dominated by either *Q. alba* or *Q. rubra* each had two species of about equal rank in second place. Under these circumstances, the most logical arrangement of stands is that indicated in the table, which shows a decreasing order of *Q. velutina* and an increasing order of *A. saccharum*, with *Q. alba* and *Q. rubra* in intermediate positions.

TABLE II. *Average importance value (IV) and constancy % of trees in stands with given species as the leading dominant*

(For species with highest importance potential only—80 stands)

Species	Leading dominant in stand			
	<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Q. velutina</i>				
Average IV	165.1	39.6	13.6	0
Constancy %	100.0	72.3	38.3	0
<i>Q. alba</i>				
Average IV	69.9	126.8	52.7	13.7
Constancy %	100.0	100.0	97.1	66.7
<i>Q. rubra</i>				
Average IV	3.6	39.2	152.3	37.2
Constancy %	25.0	94.5	100.0	76.3
<i>A. saccharum</i>				
Average IV	0	0.8	11.7	127.0
Constancy %	0	5.6	29.4	100.0

TABLE III. *Average importance value (IV) and constancy % of trees in stands with given species as the leading dominant*

(Eleven species of intermediate importance potential—80 stands)

Species		Leading dominant in stand			
		<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Q. macrocarpa</i>	IV	15.6	3.5	4.2	0.1
	C %	50.0	38.9	20.6	4.8
<i>Prunus serotina</i>	IV	21.4	21.8	5.9	1.4
	C %	87.5	89.0	64.8	19.0
<i>Carya ovata</i>	IV	0.3	8.8	5.2	5.9
	C %	12.5	61.2	38.3	33.3
<i>Juglans nigra</i>	IV	1.5	1.2	2.2	1.9
	C %	12.5	11.1	20.6	23.8
<i>Acer rubrum</i>	IV	3.9	2.3	2.4	1.0
	C %	12.5	33.3	23.5	4.8
<i>Juglans cinerea</i>	IV	0	2.7	1.7	4.8
	C %	0	11.1	20.6	47.6
<i>Fraxinus americana</i>	IV	0	1.9	5.1	7.6
	C %	0	11.1	20.6	42.8
<i>Ulmus rubra</i>	IV	4.6	7.7	8.3	32.5
	C %	25.0	27.8	53.3	85.7
<i>Tilia americana</i>	IV	0.3	5.9	19.0	33.0
	C %	12.5	16.7	73.5	100.0
<i>Carya cordiformis</i>	IV	2.5	5.8	4.1	8.2
	C %	12.5	33.3	41.2	66.7
<i>Ostrya virginiana</i>	IV	0	2.4	5.5	16.2
	C %	0	22.2	41.2	95.3

TABLE IV. Average frequency and constancy % of understory species in stands with given tree species as the leading dominant (80 stands)

Species	Leading dominant in stand			
	<i>Q. velutina</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>A. saccharum</i>
<i>Cornus foemina</i>				
Average frequency %	20.0	23.9	16.2	0.0
Constancy %	66.6	100.0	67.8	12.5
<i>Sanguinaria canadensis</i>				
Average frequency %	0	7.5	7.8	14.0
Constancy %	0	35.7	46.5	50.0
<i>Laportea canadensis</i>				
Average frequency %	0	0	0.2	9.4
Constancy %	0	0	3.6	37.5

This ranking of the stands seemed to be in agreement with the general descriptions of the forest series reported for the region and thus gave promise of further fruitful investigation. Accordingly, the same method (based on groups with *Q. velutina*, *Q. alba*, *Q. rubra* and *A. saccharum* as leading dominants) was used to calculate average constancy percentages and importance values for a series of other tree species of intermediate importance potential. The results as shown in Table III have been arranged in a natural order in that those first in the list (*Q. macrocarpa*, *Prunus serotina*, *Carya ovata*) seem to be allied to *Q. velutina* and *Q. alba*, while those placed last (*Carya cordiformis*, *Tilia americana*, *Ostrya virginiana*) are clearly associated with *Acer saccharum*.

Average frequency and constancy

values for several herbs and shrubs were determined for the same groups of stands (Table IV); they showed the same types of distribution, with optimum values in a particular group for each species. Measurements of certain soil characters were also averaged by these groups (Fig. 2) and they too showed similar trends.

The alignment of lesser species with the four major dominant trees shown in Tables III and IV is not very precise, since it does not separate those species which may be associated with the same major dominant. To make further separation possible, the stands were classed into eight groups, based on the two leading dominants in order of their importance values. Thus the stands which had *Q. alba* as the main dominant were split into two subgroups—those with *Q. velutina* as the second most important tree and those with *Q. rubra* as the second tree. Constancy percentages and average importance values were calculated for all species in each subgroup. Some of the results are given in Figure 3. They are arranged with the sequence of the groups based on the information in Table II and with the individual species arranged in order from those most closely associated with *Q. velutina* to those most allied to *Acer saccharum* as shown by the position of the stands in which they reach optimum importance. On the basis of this information, the

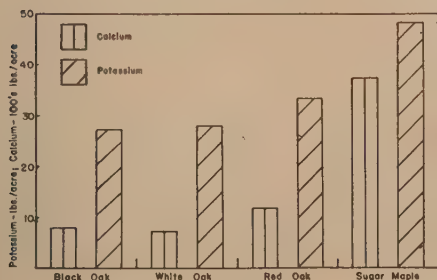


FIG. 2. Available potassium and calcium in the A₁ soil horizon of stands in which the indicated species are the leading dominants.

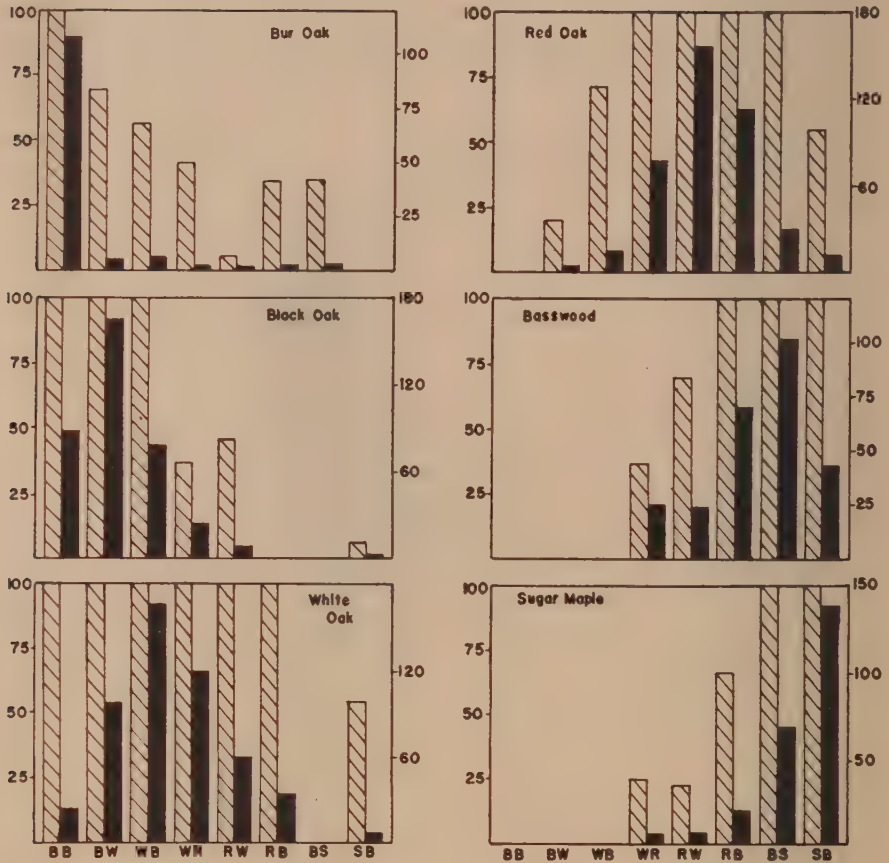


FIG. 3. Average importance value (solid bars) and constancy % (hatched bars) for major species in stands grouped according to the two leading dominants. The scales on the left ordinates are constancy percentages, those on the right ordinates are average importance values. The group of stands are indicated by the paired letters below the graphs, where BB represents the stands in which Bur Oak (*Q. macrocarpa*) is the leading dominant and Black Oak (*Q. velutina*) is the second leading dominant; BW represents stands with Black Oak as first dominant and White Oak (*Q. alba*) as second dominant; WB with White Oak leading and Black Oak second; WR with White Oak leading and Red Oak (*Q. rubra*) second; RW with Red Oak first and White Oak second; RB with Red Oak first and Basswood (*Tilia americana*) second; BS with Basswood-first and Sugar Maple (*Acer saccharum*) second; and finally SB with Sugar Maple the leading dominant and Basswood second.

species can be arranged in the following order, from pioneer to climax species: *Quercus macrocarpa* → *Q. velutina* → *Prunus serotina* → *Q. alba* → *Carya ovata* → *Juglans nigra* → *Q. rubra* → *Acer rubrum* → *Fraxinus americana* → *Tilia americana* → *Juglans cinerea* → *Carya cordiformis* → *Ulmus rubra* → *Ostrya virginiana* → *Acer saccharum*.

The method of leading dominants thus served to arrange the stands into groups which showed a reasonable phytosociological pattern but it could not demonstrate the existence of discrete communities since it was based on an artificial, even though objective, choice of unifying species. In addition, it suffered from the vagaries resulting from the calculation

of averages from differing numbers of stands in each group or subgroup. It seemed desirable, therefore, to treat the stands individually, rather than to average them in groups.

To facilitate handling this large amount of data, the moveable strip method was devised. A strip of opaque white celluloid, $\frac{1}{4}$ inch wide and 10 inches long, was prepared for each stand. The importance value of each tree species in the stand was shown on this strip by means of colored marks, located on the basis of the scale of importance values from 0 to 300. By this method the kinds and relative importance of the tree species in any stand could be determined at a glance, and by placing the strips side by side in a suitable frame, comparison of many stands could be accomplished by inspection. Natural groupings of tree species might be expected to become apparent, if any existed.

The most enlightening arrangement of stands was made on the basis of the information gained from the leading dominant method. The strips were placed so that the importance values of *Q. velutina*, *Q. alba*, *Q. rubra* and *A. saccharum* most nearly approached the order of these species which was indicated in Figure 3. This subjective procedure could not be very precise, but a good approximation was achieved (Fig. 4) as shown more clearly by Figure 5, where the same data are averaged by successive groups of

five stands, smoothed by the formula: $(a + 2b + c)/4$.

The other species were not used in establishing this original rank, but they were found to be distributed in characteristic positions when their importance values in each stand were arranged in the order established above. Figure 6 shows distributions of *Q. macrocarpa*, *Prunus serotina*, *Tilia americana* and *Ostrya virginiana*. *Quercus macrocarpa* and *Prunus serotina*, on the basis of their distribution relative to the major species, are seen to be more nearly akin to the pioneer species, while *Ostrya virginiana* and *Tilia americana* are seen to approach the climax species, thus substantiating the results of Figure 3. The remainder of the species are distributed similarly when plotted in this way.

The relative position in which each species approaches its optimum development can be fixed by means of diagrams similar to Figures 5 and 6 where sufficient data are available. The breadth of any of the figures and the absolute position of the mode would be changed if more stands were added to the series. However, the relative position remains essentially the same once a sufficient number of points is available. At the end of the first year's study, with data available for only 60 stands, the curves for the major species were well established in the same relative positions as given by the final data on 95 stands.

A study of all the figures shows that each species has a minimum, an optimum and a maximum point for development, with the points located by reference to similar states for other species. The only exceptions are *Q. macrocarpa* and *Acer saccharum*, which lack one of the cardinal points due to their location at opposite ends of the series within the limits of the study. It is to be emphasized that the optimum points for each species are purely relative. The strip method can show that *Juglans nigra* reaches its best development in forest stands which are intermediate between

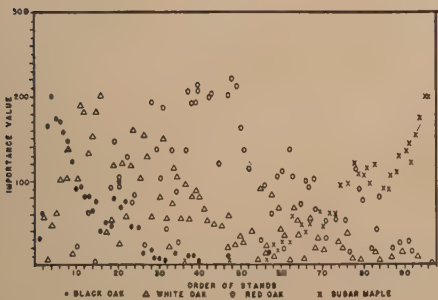


FIG. 4. Importance values of four major species in individual stands arranged in an order most closely approaching that shown in Fig. 3.

stands dominated by *Q. alba* and others dominated by *Q. rubra* but it cannot give a precise measure of the difference. Nevertheless, the arrangement of stands provided by this method shows that the tree species found in the upland hardwoods of southern Wisconsin form a continuous series, with overlapping ranges but distinct conditions for optimum development of each species. No discrete groupings of species are apparent; rather, the entire assemblage forms a continuum.

Climax adaptation numbers

The above results indicate that each tree species reaches its optimum development in stands whose position is fixed in a definite relationship to the other tree species. The sequence of the species in this pattern is such that pioneer species are at one end and climax species at the other. Pioneer and climax are here used in their adjectival sense and refer to the entire syndrome of specific physiological attributes which enables the one to live in the high light, variable moisture and immature soil conditions of initial stands and the other in the low light, medium moisture and mature soil conditions of the terminal forests.

The results of this study, as well as those of other investigations in this area, indicate that *Acer saccharum* is the tree species best equipped to persist in the terminal forests of the area. All other species are less efficient in this respect, and their relative degree of "climaxness"

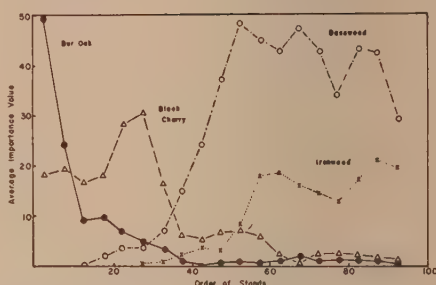


FIG. 6. Importance values of four lesser species, arranged in the order given in Fig. 4 and averaged by successive groups of 5 stands.

may be evaluated by the spatial relations of their optimum development curves as illustrated in Figures 5 and 6. Thus *Tilia americana*, whose highest importance values are reached in stands near the *A. saccharum* end of the pattern, is better adapted to terminal forest conditions than *Q. rubra*, with a peak closer to the middle of the series, while *Q. macrocarpa*, which is most important in stands remote from those dominated by *A. saccharum*, is the least well adapted.

Using *Acer saccharum* as a standard, all other species can be rated on the basis of the distance of their optimum stands from those dominated by *Acer*. The rating was accomplished by arbitrarily assigning a relative value of ten to *A. saccharum* and lesser numbers to the other species according to their position, as shown in Table V. Those species designated by an asterisk are tentatively placed with an approximate value inasmuch as they occur only rarely in the samples and thus their position is not clearly established by the few points available.

The choice of suitable words to designate the two ecologically distinct ends of the series is a troublesome one. The word "climax" for the terminal end is especially doubtful, since it already has a plethora of meanings and probably would not be defined the same by any two practicing ecologists. It has been suggested that the term "mesophily," as employed by Dansereau (1943), be used in the

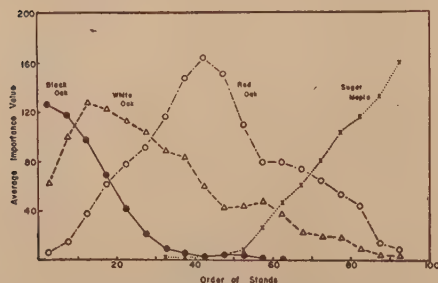


FIG. 5. Same data as in Fig. 4 averaged by successive groups of 5 stands.

TABLE V. *Scientific and common names of tree species found in stands studied, with the climax adaptation numbers of each*

Scientific name	Common name	Climax adaptation number
<i>Quercus macrocarpa</i> Michx.	Bur oak	1.0
<i>Populus tremuloides</i> Michx.	Trembling aspen	1.0
* <i>Acer negundo</i> L.	Boxelder	1.0
<i>Populus grandidentata</i> Michx.	Large-tooth aspen	1.5
<i>Quercus velutina</i> Lam.	Black oak	2.0
<i>Carya ovata</i> (Mill.) K. Koch	Shagbark hickory	3.5
<i>Prunus serotina</i> Ehrh.	Black cherry	3.5
<i>Quercus alba</i> L.	White oak	4.0
<i>Juglans nigra</i> L.	Black walnut	5.0
<i>Quercus rubra</i> L.	Red oak	6.0
<i>Juglans cinerea</i> L.	Butternut	7.0
* <i>Ulmus thomasi</i> Sarg.	Rock elm	7.0
* <i>Acer rubrum</i> L.	Red maple	7.0
<i>Fraxinus americana</i> L.	White ash	7.5
* <i>Gymnocladus dioica</i> (L.) Koch	Kentucky coffee tree	7.5
<i>Tilia americana</i> L.	Basswood	8.0
<i>Ulmus rubra</i> Muhl.	Slippery elm	8.0
* <i>Carpinus caroliniana</i> Walt.	Blue beech	8.0
* <i>Celtis occidentalis</i> L.	Hackberry	8.0
<i>Carya cordiformis</i> (Wang) K. Koch	Yellowbud hickory	8.5
<i>Ostrya virginiana</i> (Mill.) K. Koch.	Ironwood	9.0
<i>Acer saccharum</i> Marsh	Sugar maple	10.0

* Climax adaptation number of these species is tentative, because of their low frequency of occurrence in this study.

present case instead of climax. It is true that the climax plants here discussed are extreme mesophytes, in the sense that they achieve optimum development only in habitats of medium and relatively constant conditions of both atmospheric and edaphic moisture. However, it is equally true and probably of greater significance that these climax plants are shade-loving plants (sciophytes) able to grow and reproduce in conditions of very low light intensity. For the most part they are also plants of high nutrient demands, with tendencies toward partial heterotrophism. They are therefore not median with respect to light or nutrition and the use of the word "mesophily" might carry unfortunate connotations. It would involve an extension of meaning as great as in the case of "climax." What is perhaps needed is a word to encompass all of those adaptive physiological and morphological characters that differentiate plants of initial stands from plants of terminal stands. In the absence of such a word, we have deemed it best here to use the phrase "climax adaptation" as a tentative description of these characters, and to call the relative values as-

signed to each species "climax adaptation numbers." High numbers indicate good adaptation to all of the environmental factors present in terminal stands while low numbers indicate adaptation to the conditions of initial stands. This admittedly unsatisfactory compromise at least has the merit that it does not unduly emphasize one factor in an obviously multiple factor situation even though it does further burden the already overworked word climax. "Succession number" has been suggested, but it is inadequate, since an intermediate stage in the series may be reached by retrogressive as well as by successional processes.

A comparison of these climax adaptation numbers with the shade tolerance ratings of foresters indicates that they are roughly parallel. This is not unexpected, since the characteristics that contribute to great shade tolerance are largely the same as those that make for persistence in terminal stands. The method used here in establishing the climax adaptation numbers may offer a supplement to the usual procedures for the subjective determination of

shade tolerance. It offers greater possibility of refinement than the coarse, qualitative estimates generally used. It must be recognized, however, that the application of this type of rating is only feasible within the bounds of a single floristic province, since shade tolerance as measured by the adaptation number of a species may vary in other areas with different component floras.

Vegetational continuum index

To establish a basis for evaluating forest stands in terms of their total tree composition it was decided to use the climax adaptation number of each tree species as a means of weighting its importance value as determined from the sampling data. The adaptation number of each species (as given in Table V) was multiplied by its importance value in a particular stand. The products were added and the resultant weighted total used as a basis of placing the stand in its proper relation to other stands. The maximum possible range of these weighted numbers is 2,700 units from 300 to 3,000. A stand composed entirely of *Q. macrocarpa* or a mixture of *Q. macrocarpa* and *Populus tremuloides* would have a sum of 300; a stand composed solely of *A. saccharum* would have a sum of 3,000. A stand consisting of mixtures of species whose climax adaptation numbers lie between one and ten would have a sum somewhere between these extremes. This range of

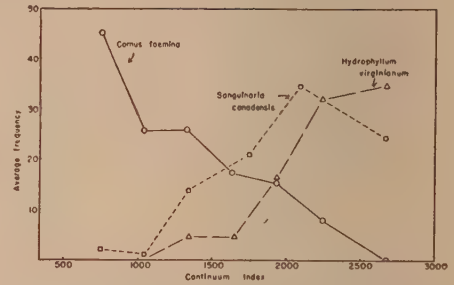


FIG. 8. Average frequency values of three herbs, arranged in order of continuum index.

weighted numbers is termed the *vegetational continuum index*. A continuum index value was calculated for each stand in the study. When the celluloid strips for each stand were arranged in the numerical sequence given by these index values (Fig. 7) it was found that the distributional pattern for each of the tree species retained the same relative position as before.

The vegetational continuum index is actually a means of utilizing all of the tree species in a stand to express the position of that stand on a gradient. Major importance in assessing the position of a stand falls upon those species which have a high importance value but each of the other tree species contributes in some degree.

Tree reproduction is distributed on the vegetational continuum index in a pattern similar to that of the mature trees. The reproduction should possibly be used to further weight the position of a stand in the vegetational continuum index, but, as indicated earlier, the sampling method used in this study gave inadequate data on saplings in most cases and therefore such weighting was not attempted.

Herb and shrub species which played no part in developing the vegetational continuum index were found to be distributed on it in patterns similar to those of the tree species. The distributions of certain shrub and herb species is illus-

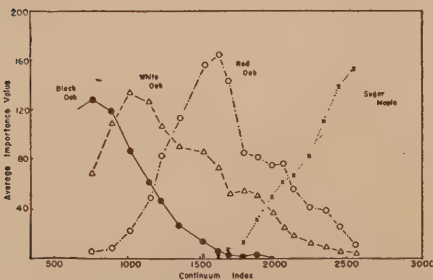


FIG. 7. Importance values of four major species arranged in numerical order of continuum index and averaged by successive groups of 5 stands.

trated in Figure 8. They are found to form curves with characteristic minimum, optimum and maximum points for development. These curves locate the lesser species relative to the tree species and to each other. Some herbaceous species, unlike most trees, are found to cover the entire range of stands, but it is nevertheless possible to predict with reasonable accuracy the important herb species to be found in stands in any given range of the vegetational continuum index.

Soil factors also may be related to the forest cover by means of the vegetational continuum index. The relation of exchangeable calcium and of soil reaction to the index is shown in Figures 9 and 10. The values in these graphs were

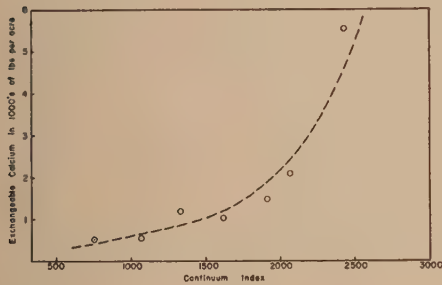
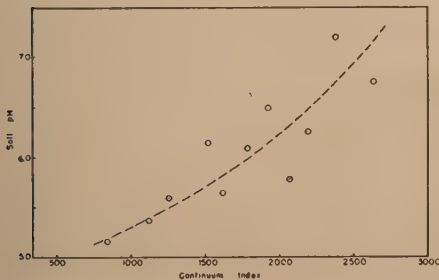


FIG. 9.

obtained by averaging successive groups of three stands for which data were available. Similar correlations were obtained with the water retaining capacity and the organic matter content.

FIG. 10. Acidity of the A₁ layer in stands arranged on the continuum index.

DISCUSSION

Three possibilities as to the nature of the upland hardwood forests of this area may be postulated. The first of these is that the forests represent an amorphous collection of plants in which no units or patterns are discernable. In other words, they are chance aggregates according to the viewpoint of Mason (1947) and are dependent solely on a "coincidence of tolerance" between plants and environment. The presence of a pattern definable in terms of tree composition and the demonstration that trees and other plants are not found together in chance mixtures but in a rather definite pattern would indicate that this interpretation is not tenable in the present case.

Secondly, one could maintain that these forests represent several discrete communities, distinguishable from each other by boundaries which are reasonably distinct in terms of the measurements available to the plant ecologist. If this were true, then determination of the relative sociological importance of the trees in each stand should show that certain groups of tree species reach their optimum development in the same stands, while other groups occur together in other stands. If the boundaries between communities are actually distinct, then the species of one group should never occur as important members of another group. The results of this study indicate that such a discrete grouping of species does not occur in Wisconsin. Rather, each species reaches a high level of importance in only a few stands, with no groups of two or more species showing optimum development in the same stands.

It is thus necessary to accept the third possibility, namely that the upland hardwoods of southwestern Wisconsin represent a continuum in which no clearly defined subdivisions are discernable but in which a definite gradient is exhibited. If this is truly the case then the entire physiognomic upland hardwood forest is to be interpreted as an entity (or por-

tion of an entity) without discrete subdivisions. The failure of any one or any group of the environmental factors measured to indicate any separation substantiates the conclusion of unity based on the tree data. The presence in certain of these environmental factors of some indication of a gradient or trend related to the tree gradient is further indication that these forests represent a continuous cline from initial stages composed of pioneer species to terminal stages composed of climax species.

This conclusion would appear to substantiate the individualistic association hypothesis of Gleason (1926) and its emendation by Cain (1947). It differs, however, in that "*unlimited* variables, combinations and permutations" (Cain) do not occur. All things are not possible, only some, and these possible permutations seem to follow a pathway prescribed by the physiological potentialities of the available flora within the limits of the existent physical environment as modifiable by that flora. Within a given floristic province, the amplitude of environmental tolerance of each species is more limited than the full range of environment in that province. Furthermore, although the tolerance range of each species may overlap that of many other species, the range for optimum development of each species is different from that of all other species. There are, therefore, no groups of tree species which regularly occur together and only together, except for accidental duplications of narrow environmental ranges. Rather, tree species occur in a continuously shifting series of combinations with a definite sequence or pattern, the resultant of a limited floristic complement acting on, and acted upon by, a limited range of physical environmental potentialities. Such a gradient of communities is here called a vegetational continuum, to differentiate it clearly from the controversial concept of a plant association. As applied to forests, it is similar in scope to the "sylvan continuum" of Darling (1949).

The geographical limits of this continuum outside of Wisconsin are not known at present, but it appears that southeastern Minnesota, northeastern Iowa and northern Illinois are definitely included. There are indications that the upland forests on the southern border of the prairie peninsula are similar also, especially those in Missouri, Nebraska (Aikman 1926), Arkansas (Arend and Julander 1948) and Kentucky. This is perhaps to be expected on the basis of climatic similarities (Borchert 1950). The continuum throughout is intimately associated with the prairie-forest border. Its major trees are better adapted to xeric conditions, particularly those associated with periodic severe summer droughts, than are most other species of the deciduous forest. It has borne the brunt of repeated prairie advances in post-Wisconsin time and possibly in earlier interglacial periods as well (Lane 1941, McComb and Loomis 1944). As a result, it is probably simpler in both floristic composition and developmental pattern than the forest aggregations farther east and south. It is recognized that this simplicity was an important factor in the recognition of the continuum pattern and that similar patterns may be more difficult to ascertain in other regions of greater floristic variety.

If the vegetation of a particular physiognomy on a particular topography in a particular floristic province (*i.e.*, deciduous hardwood forests on the uplands of southwestern Wisconsin) forms a continuum without identifiable individual segments, as is the contention of the present paper, then certain far-reaching implications are apparent. Without at this time entering the perennial argument concerning the relative scope of the word "association" as used by American and European workers, it is obvious that both groups usually apply it to discrete communities which are thought to be recognizable as distinct entities in the field. It is on this characteristic that the whole series of "synthetic" characters of

plant communities was erected by Rübel (1922), Braun-Blanquet (1927) and other European workers. Such well-established community measures as presence, constancy, and fidelity become of greatly restricted value when applied to stands which form a continuum. For example, in the present case, a number of herbs are known which may be found in almost every initial stand in which the leading dominant is *Quercus velutina* and thus would have a high degree of presence or constancy in those stands. All of them, however, also occur in lesser amounts and in a smaller percentage of the stands which are dominated by *Q. alba*. This diminution continues in the *Q. rubra* stands and most of the species become very rare or absent in the terminal *Acer saccharum* forest. A similar situation in reverse exists for a group of species most common in the *Acer* stands. The absolute value of presence or constancy, therefore, is determined almost solely by the amplitude allowed by the investigator in his choice of stands to be studied. If a large portion of the continuum is used, then all species except the most ubiquitous and least demanding have very low values of presence and constancy. These ubiquitous species are commonly found in nearby non-related assemblages and hence are of very low value as community indicators in any case. As the portion of the continuum used becomes restricted in scope, then the presence and constancy values increase in magnitude. As we have seen, however, scarcely any two stands exist which have precisely the same complement of tree species, to say nothing of the more numerous herbs, and hence, presence and constancy values rarely achieve truly high levels.

It appears probable from preliminary observations that the lowland forests (which receive at least temporary accumulations of run-off water) of this area will eventually prove to be part of the same continuum herein discussed. If this should indeed be the case, then the

synthetic characters would be still further reduced in usefulness, since their arithmetic values would be of very low magnitude. Presence and constancy may continue to maintain their useful roles in phytosociology if each investigator accompanies them with a detailed account of the limits set by him on the range of communities included within his study. When used in this way, the synthetic characters may be very valuable, particularly in comparative studies, as between grazed and non-grazed woodlots or the like.

It is hoped that the concept of a vegetational continuum and the methods for its analysis as developed in this paper will prove to be widely applicable to the forest stands of other regions. Whether or not all floristic provinces have similar continuous gradients rather than recognizably discrete communities is not known at present, although a few studies based on the analysis of many stands in a single region (Hanson and Whitman 1938; Whittaker 1948; Allen 1950; Potzger 1950) clearly indicate that similar continua are present. Dyksterhuis (1949) also shows a continuously varying composition of grassland under the impact of overgrazing which is essentially similar to the forest continuum here described.

In those areas in which its construction is possible, the vegetational continuum index offers a new approach to ecological studies of many types. It may be used to describe local deviations in tree composition such as occur when pioneer species enter spot openings in a mature forest resulting from a restricted fire or other disturbance and such other situations as are included in the "gap phase" concept of Watt (1947). Autecological studies of an herbaceous species may be conducted in stands which are known to be optimum for the development of that species and comparative life history studies of groups of species may be made readily in stands known to be similar on the basis of trees and soils. The index

provides a more detailed framework for the study of the relation of random and contagious distributions of herbaceous species in relation to age of occupancy as discussed by Whitford (1949). Mammal, bird, insect or other animal populations, their fluctuations and interrelationships, are all inseparably interwoven with plant communities. One of the major difficulties heretofore encountered in studies of natural animal populations has been the lack of an adequate means of delimitation of the nature of the plant segment of the habitat complex. The vegetational continuum index affords a more accurate means of describing this habitat factor and in addition immediately places a stand in its proper relation to other stands. As further information is collected on the correlations between the physical factors of the environment and the index and on the relations of the microbiota or other special groups of organisms to the index, it will be possible to summarize a very considerable amount of information by means of an index number. There is no thought here that the index will serve as the final touchstone of phytosociologists, nor that the complex of physical and biological agents of importance in a community can possibly be reduced to a single number. The index rather should serve as a framework upon which a great amount of independently derived information may be arranged and interrelated.

SUMMARY

1. The upland hardwood forests of the prairie-forest floristic province of southwestern Wisconsin were studied by means of a random sampling of undisturbed stands distributed through 29 counties covering an area 160 miles by 230 miles. Data on tree, shrub, and herb composition were obtained in 95 stands by the random pairs method of sampling. Soil acidity, nutrient concentration and moisture constants were also determined for these stands.

2. The relative ecological importance of each tree species in each stand was expressed by a summation index of the relative frequency, relative density and relative dominance herein called the *importance value*. This value has a constant total of 300 for each stand.

3. Four tree species (*Quercus velutina*, *Q. alba*, *Q. rubra* and *Acer saccharum*) attained an average importance value in all stands much higher than that of any other species. When the stands were arranged into groups each dominated by one of these four species, it was found that each of the lesser tree species was associated with one of the groups. Further breakdown of the stands into subgroups according to the second most important species, resulted in a more accurate alignment of all species into a series beginning with the pioneer species, *Quercus macrocarpa*, *Populus grandidentata*, and *Quercus velutina*, and ending with the climax species *Ostrya virginiana* and *Acer saccharum*. Each species reached optimum development at a given point along this series, but no groups of species were found which achieved their peak in the same stands. Thus no discrete communities could be detected on the basis of the leading dominants in the stands.

4. Use of a strip method for visual comparison of the importance values of all species in each stand resulted in a ranking or order of stands which agreed with the order obtained from the leading dominants. The initial stands in the rank were composed of shade-intolerant, non-mesic, pioneer species, while the terminal stands contained the very shade-tolerant, mesic climax species. Upon the assumption that *Acer saccharum* was the most successful species in the terminal forests, it was possible to arrange all other tree species in a descending order according to the position of the stands in which they reached optimum development, relative to the stands containing *Acer saccharum*. Arbitrary numbers from one to ten, called *climax adaptation*

numbers, were assigned to the species to indicate the degree to which they approach the climax *Acer* in autecological characteristics. For the more important trees of the region, the adaptation numbers are as follows: *Quercus macrocarpa*—1.0, *Quercus velutina*—2.0, *Carya ovata*—2.5, *Prunus serotina*—3.5, *Quercus alba*—4.0, *Quercus rubra*—6.0, *Ulmus rubra*—7.0, *Tilia americana*—7.5, *Ostrya virginiana*—8.0, and *Acer saccharum*—10.0.

5. The climax adaptation numbers were used as a means of weighting the importance values of each species in a stand, as determined by field sampling. The summation of these weighted numbers resulted in an index which served to locate the stand along a gradient. All species present contributed to the index, with the greatest effect exerted by the dominant species. On this basis, the 95 stands studied were distributed uniformly between an index value of 632 and a value of 2,650 (out of a possible range from 300 to 3,000). No distinct groups of stands were apparent—rather the entire series of communities formed a continuum in which a definite gradient was exhibited from initial stages composed of pioneer species to terminal stages composed of climax species. Such a gradient of communities is here called a *vegetational continuum*.

6. Herb and shrub species were found to be distributed in typical patterns when their frequencies were plotted against the continuum index. Each of these understory plants was restricted to a particular range on the index—each reached optimum developments only within a particular group of closely related stands. Various measurements of soil properties showed a good correlation with the index. This was especially true of the concentration of available calcium, the water retaining capacity and the organic matter content of the A_1 soil layer.

7. It is suggested that the vegetational continuum index may be a useful tool for the coordination of much independ-

ently derived information on animal populations, microbiota, and physical factors of the environment.

LITERATURE CITED

- Aikman, J. M. 1926. Distribution and structure of the deciduous forest in eastern Nebraska. Univ. Nebraska Studies 26: 1-75.
- Aikman, J. M., and A. W. Smelser. 1938. The structure and environment of forest communities in central Iowa. Ecology 19: 141-170.
- Allan, P. F. 1950. Ecological basis for land use planning in Gulf Coast marshlands. Jour. Soil and Water Conserv. 5: 57-62, 85.
- Anderson, Edgar. 1941. The technique and use of mass collections in plant taxonomy. Ann. Missouri Bot. Garden 28: 287-292.
- Arend, J. L., and O. Julander. 1948. Oak sites in the Arkansas Ozarks. Arkansas Agr. Exp. Sta. Bull. 484: 1-42.
- Borchert, J. R. 1950. The climate of the central North American grassland. Ann. Assoc. Amer. Geog. 40: 1-39.
- Braun-Blanquet, J. 1928. Pflanzensoziologie. Julius Springer. Berlin.
- Bruncken, E. 1900. On the forest conditions in the vicinity of Milwaukee. Bull. Wisconsin Nat. Hist. Soc. 1: 179-184.
- Cain, S. A. 1947. Characteristics of natural areas and factors in their development. Ecological Monog. 17: 185-200.
- Chamberlain, T. C. 1877. Native vegetation. Geology of Wisconsin 2: 176-187.
- Cheney, L. S. 1894. Is forest culture in Wisconsin desirable? Trans. Wisconsin State Hist. Soc. 24: 163-170.
- Clark, O. R. 1926. An ecological comparison of two types of woodland. Proc. Iowa Acad. Sci. 33: 131-134.
- Clements, F. E. 1905. Research methods in ecology. Univ. Publ. Co., Lincoln, Neb.
- Cottam, G. 1949. The phytosociology of an oak woods in southwestern Wisconsin. Ecology 30: 271-287.
- Cottam, G., and J. T. Curtis. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected individuals. Ecology 30: 101-104.
- Curtis, J. T., and H. C. Greene. 1949. A study of relic Wisconsin prairies by the species-presence method. Ecology 30: 83-92.
- Curtis, J. T., and R. P. McIntosh. 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31: 434-455.
- Dansereau, P. 1943. L'erabliere Laurentienne. Can. Jour. Res. 21: 66-93.
- Darling, F. F. 1949. History of the Scottish forests. Scottish Geog. Mag. 65: 132-137.
- Daubenmire, R. F. 1936. The "Big Woods"

- of Minnesota: Its structure, and relation to climate, fire and soils. *Ecological Monog.* 6: 235-268.
- DeForest, Howard.** 1921. The plant ecology of the Rock River woodlands of Ogle Co., Illinois. *Ill. State Acad. Sci. Trans.* 14: 152-193.
- Desmarais, Yves.** 1948. Dynamics of leaf variation in the sugar maples. Ph.D. thesis. Univ. of Wisconsin.
- Dyksterhuis, E. J.** 1949. Condition and management of range land based on quantitative ecology. *Jour. Range Manage.* 2: 104-115.
- Eggler, W. A.** 1938. The maple-basswood forest type in Washburn County, Wisconsin. *Ecology* 19: 243-263.
- Egler, F. E.** 1947. Arid southeast Oahu vegetation, Hawaii. *Ecological Monog.* 17: 383-435.
- Fassett, N. C.** 1941. Mass collections: *Rubus odoratus* and *R. parviflorus*. *Ann. Missouri Bot. Gard.* 28: 299-374.
- Fuller, G. D., and P. D. Strausbaugh.** 1919. On the forests of LaSalle Co., Ill. *Ill. State Acad. Sci. Trans.* 12: 246-272.
- Gleason, H. A.** 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7-26.
- Griggs, R. F.** 1914. Observations on the behavior of species at the edge of their range. *Bull. Torrey Bot. Club* 41: 25-49.
- Hanson, H. C., and W. Whitman.** 1938. Characteristics of major grassland types in western North Dakota. *Ecological Monog.* 8: 57-114.
- Lane, G. H.** 1941. Pollen analysis of interglacial peats of Iowa. *Iowa Geol. Survey* 37: 233-262.
- Lapham, I. A.** 1852. Woods of Wisconsin. *Trans. Wisconsin State Agr. Soc.* 2: 419-434.
- Marks, J. B.** 1942. Land use and plant succession in Coon Valley, Wisconsin. *Ecological Monog.* 12: 113-134.
- Mason, H. L.** 1947. Evolution of certain floristic associations in western North America. *Ecological Monog.* 17: 201-210.
- McComb, A. L., and W. E. Loomis.** 1944. Subclimax prairie. *Bull. Torrey Bot. Club* 71: 46-76.
- McIntosh, R. P.** 1950. Pine stands in southwestern Wisconsin. *Trans. Wis. Acad. of Sci., Arts, Letters.* 40: 243-258.
- Pammel, L. H.** 1904. Forestry conditions in western Wisconsin. *Forestry & Irrig.* 10: 421-426.
- Potzger, J. E.** 1950. Forest types in the Versailles State Park area, Indiana. *Amer. Midland Nat.* 43: 729-746.
- Raunkiaer, C.** 1934. The life forms of plant and statistical plant geography. Oxford, Clarendon Press. London.
- Raup, H. M.** 1947. Some natural floristic areas in boreal America. *Ecological Monog.* 17: 221-234.
- Rübel, E.** 1922. *Geobotanische Untersuchungs-methoden.* Berlin.
- Salamun, P. J.** 1950. The interpretation of variation in populations of *Spiraea tomentosa*, *Brachyelytrum erectum*, *Osmorhiza claytoni*, and *Osmorhiza longistylis*. Ph.D. thesis. Univ. of Wisconsin.
- Snedecor, G. W.** 1946. *Statistical methods.* Fourth Ed. Iowa State College Press. Ames.
- Stearns, F.** 1951. The composition of the sugar maple-hemlock-yellow birch association in northern Wisconsin. *Ecology* 32: 245-265.
- Stout, A. B.** 1944. The bur oak openings of southern Wisconsin. *Trans. Wisconsin Acad.* 36: 141-161.
- Wagner, R. D.** 1947. The ecological composition of an oak-maple subclimax forest in Jefferson County, Wisconsin. M.S. thesis. Univ. of Wisconsin.
- Watt, A. S.** 1947. Pattern and process in the plant community. *Jour. Ecology* 35: 1-22.
- Weaver, J. E., and F. E. Clements.** 1938. *Plant Ecology.* McGraw-Hill. New York.
- Whitford, P. B.** 1951. Estimation of the ages of hardwood stands in the prairie-forest border region. *Ecology* 32: 143-146.
- . 1949. Distribution of woodland plants in relation to succession and clonal growth. *Ecology* 30: 199-208.
- Whittaker, R. H.** 1948. A vegetation analysis of the Great Smoky Mountains. Ph.D. thesis. Univ. of Illinois.
- Yapp, R. H.** 1922. The concept of habitat. *Jour. Ecol.* 10: 1-17.

CLUTCH-SIZE AND EGG MORTALITY OF KENT ISLAND EIDERS¹

RAYMOND A. PAYNTER, JR. ,

Yale University, New Haven, Connecticut

INTRODUCTION

At the turn of the century the American eider (*Somateria mollissima dresseri*) was nearly exterminated as a breeding species along the coast of Maine and southern Canada, although at one time it was one of the most common ducks breeding in the region. Presumably, the marked decrease in the population was brought about by intensive year-round hunting and by gathering of eggs for food.

Gross (1938, 1944) has given a complete historical review of the breeding status of the eider in Maine and southern New Brunswick, which need not be repeated in detail. In brief, 1907 appears to have been the low point of the population in Maine when only two pairs were known to have bred on the entire coast. Under rigid protection, during the succeeding forty years, the eider population grew at an increasingly rapid rate. By 1931 Norton and Allen found over fifty nests and broods along the coast of Maine and in 1944 Gross estimated a breeding population of over 2,000 pairs in the same area.

In a relatively small area around Grand Manan Island, New Brunswick, the increase in the breeding population of the eider has been even more pronounced. In 1908 Brownson reported a dozen pairs nesting in the vicinity of Grand Manan. By 1936 (Pettingill 1939), the population had grown to approximately 185 pairs in the same region and at present I estimate that at least 1,200 nests are to be found there each year.

On Kent Island, the largest of a group of three islands located about six miles to

the southeast of Grand Manan, there exists one of the greatest known concentrations of breeding American eiders. The growth of the population on Kent Island has been spectacular. In 1932 (Gross 1938), there were 178 nests and by 1937 more than three hundred nests could be located. In 1948 an estimated 750 nests were built within the huge colonies of herring gulls (*Larus argentatus smithsonianus*), Leach's petrels (*Oceanodroma l. leucorhoa*) and other sea birds (Fig. 1). Although the island consists of an area of only 150 acres, and at least 50 acres of this are not utilized by the non-passerines because of the presence of the buildings of the Bowdoin Scientific Station and extensive marshes, an estimated 35,000 or more birds of several species breed there each summer. During the post-breeding season and shore bird migrations, concentrations of 50,000 birds are not unusual. A fuller description of this magnificent bird colony may be found in the papers of Gross (1938, 1940), Pettingill (1939) and Paynter (1947, 1949).

I began field work on Kent Island in 1946, but it was not until the spring of 1948 that I was able to devote adequate time to a study of the eider. Observations were begun on May 13, 1948, and ended on August 22 when I left the island.

SPRING ARRIVAL, MATING, AND NESTING

Ernest A. Joy, resident warden at Kent Island since the establishment of the Bowdoin Scientific Station in 1935, has kept careful records of the spring arrival of the eider, the beginning of courtship, and the appearance of the first eggs. These data have been presented in Table I. There is

¹ Contribution from the Osborn Zoological Laboratory, Yale University, and No. 23 from the Bowdoin Scientific Station, Kent Island, New Brunswick, Canada.

TABLE I. *Arrival, mating and first egg dates*

Year	Arrival	First mating	First egg
'37	Apr. 7	Apr. 26	May 4
'38	Apr. 5	Apr. 16	May 9
'39	Apr. 7	Apr. 17	May 12
'40	Mar. 31	Apr. 19	May 6
'41	Mar. 28	Apr. 17	May 7
'42	Mar. 7	Apr. 28	May 8
'43	Mar. 11	No data	May 10
'44	Feb. 26	No data	May 7
'45	Mar. 2	No data	May 12
'46	Mar. 15	No data	May 6
'47	No data	No data	No data
'48	Apr. 7	No data	No data

considerable variation in the arrival dates, but it is exceedingly difficult to judge the arrival of the American eider, without collecting specimens, since during the winter months the northern eider (*Somateria mollissima borealis*) is present and considerable overlap probably occurs. The data for the first mating and eggs are more accurate, but of course these too are sub-

ject to slight errors, since it is difficult to keep so large a population under close observation.

On Kent Island most of the eiders nest on the southern end of the island, within the herring gull colony, where there are few living trees. However, numerous nests are to be found on the northern end of the island under the thick stands of spruce (*Picea mariana*) and occasionally nests are placed fully exposed along the rocky shores or in the marshes filled with flag (*Iris versicolor*).

In early May, when nesting is begun, there is little vegetation present, and most of the ducks build under fallen dead spruces or in raspberry (*Rubus idaeus*) and gooseberry (*Ribes cynosbati*) thickets, which are not yet in leaf (Fig. 2). Sometimes as many as five nests are found clustered under the branches of a single fallen spruce. These habitats afford little



FIG. 1. Many eiders nest under the fallen spruces within the herring gull colony. May 21, 1948.



FIG. 2. A poorly concealed but typical nesting site in an unleaved raspberry thicket. May 20, 1948.

concealment until well after the first of June, when the raspberry and gooseberry bushes are in leaf and the dense growth of ragweed (*Ambrosia artemisiifolia*), which covers the southern half of the island, has begun to grow. In 1948 the gooseberries came into leaf around May 21 and the raspberries leafed about two weeks later.

During the first or second week of May the first eggs are laid, as may be seen from Table I. Unfortunately, Mr. Joy was not present on the island in early May of the year of this study, and the date of the appearance of the first eggs is unknown. However, on May 13, I found two nests with clutches of five eggs. No more eggs were added on succeeding days and it is assumed that they were completed clutches, but the eggs were later destroyed by gulls and there is no way to estimate the length of time they had been incubated before being discovered. If the clutches were completed the day observations be-

gan, the first egg must have been laid on May 9, at the latest, since the eider lays a single egg each day until the clutch is completed.

Another method for estimating the date of the first egg is found in the hatching data. On June 3 the first young bird of the year was seen. Assuming that the bird hatched on this date, and with the knowledge that the incubation period is 28 days (Gross 1938), the latest the egg could have been laid would have been May 7. Both these dates are reasonable in the light of Mr. Joy's data for other years.

SELECTION OF STUDY NESTS

In 1948 the eiders were under observation while I was also conducting a survey of the herring gulls in a plot at the southern tip of the island. Two routes leading to and away from the herring gull plot were laid out and every eider nest located along these routes was inspected daily, on

my way to or from the gull study area. One route ran from the buildings of the station, at the northern third of the island, down the western side to the southern end. The return route was through the center of the island back to the buildings.

Since there is only one small grove of living spruces on the southern two-thirds of the island, few nests came under observation in such a concealed habitat. However, on Kent Island, most of the ducks nest in the more exposed areas, such as those found in the gull colony, and the nests under observation were probably a fairly representative sample of all the habitats occupied on the island.

The location of nests for study poses a number of problems. The eider does not begin to incubate until a full clutch is laid, and during the laying period the birds spend little time at the nest. Nests with incomplete clutches are seldom filled with much down and the eggs remain rather exposed, except for a few twigs and a little down which may be scratched over them before the bird returns to the water. In spite of the lack of adequate covering, the nests are small and inconspicuous and a great deal of searching is required to locate incomplete clutches.

Nests are more easily located once incubation has begun. The bird then fills the nest with down, which is conspicuous against the brown earth and the bright green vegetation, at least to the human eye. The duck is also inclined to stay at the nest until the observer is quite near. If there is ample time, the bird walks away from the nest some distance before taking to the air and, through experience, it is rather easy for one to estimate the distance it usually travels before flying. Frequently, with a few minutes' searching in suitable places, the nest can be located. In some instances, and especially when hatching is about to take place, the duck stays at the nest and flies up suddenly when approached, often discharging over the eggs highly odoriferous, semi-liquid, fecal matter. Discovery of the nest is then relatively easy. The behavior of

birds at the nest is remarkably varied. Occasionally a bird will permit close approach and sometimes even allow handling before it finally flies. The photograph in Figure 2 shows a bird which permitted me to take several photographs and actually remove her from the nest for banding before she flew.

A total of 160 nests were under observation for periods ranging from one to 30 days or more. The identification tags were torn from four nests, probably by gulls, and the nests were lost from study. Twenty-two nests were destroyed the day after they had been found and have not been considered further, thus leaving 134 nests with which to work.

However, even these 134 nests present numerous problems in their analysis. Ninety-five, or slightly more than 70 per cent of the nests, were destroyed before hatching. Some of these lost their eggs a few days after observations were begun, while other nests were under study 20 or more days before predators removed the eggs. In many cases there is no way to know whether the clutches were completed, or if they were completed, how long they had been incubated, or whether eggs had been lost from the nests before they came under observation. In spite of these difficulties, a number of methods of treatment have been applied to the data, which are believed to have provided a fairly accurate picture of the clutch-size and egg mortality of Kent Island eiders.

MEAN CLUTCH-SIZE

From Table II it may be seen that the mean number of eggs in 134 nests in 1948 was $3.56 \pm .10$. This sample includes nests that were under observation two days or more, and may include nests with incomplete clutches or those that lost eggs before they were first discovered.

In order to determine whether there was a significant number of nests under observation for so short a period that they may have had incomplete clutches, and thus brought down the mean clutch-size for the entire sample, the mean was com-

TABLE II. *Geographical variation in clutch-size of Somateria mollissima dresseri*

Locality.....	Penobscot Bay		Kent I., New Brunswick				North shore of Gulf of St. Lawrence										
	Gross 1938		This paper		Lewis 1939												
	June 7, 1933		June 12, 1947		Entire season, 1948		June 12-July 26, 1934		June 23-July 13, 1935		June 9-July 12, 1936		June 2-July 22, 1937		May 26-July 12, 1938		
Clutch-size	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	No. of nests	No. of eggs	
	1	5	2	2	3	3	2	2	5	5	1	1	13	13	6	6	
	2	23	5	10	24	48	15	30	15	30	2	4	29	58	18	36	
	3	34	102	7	21	37	111	43	129	52	9	27	71	213	40	120	
	4	37	148	10	40	45	180	81	324	110	14	56	123	492	77	308	
	5	9	45	3	15	17	85	54	270	76	12	60	100	500	95	475	
	6	2	12	1	6	6	36	11	66	7	7	7	16	96	21	126	
	7					1	7	2	14	1	1	1	2	7	14	2	
	8					1	8			1	8			2	16	3	24
	10																
Total	110	358	28	94	134	478	208	835	267	1068	38	148	355	1395	263	1119	
Mean	3.25±.10		3.36±.28		3.56±.10		4.01±.07		4.00±.06		3.89±.30		3.93±.06		4.25±.07		
Mean of all observations in locality	3.25±.10		3.53±.09		4.04±.03												

Difference between means of Kent I. and St. Lawrence region significant. $P < .001$ Difference between means of Kent I. and Maine significant. $P < .001$ Difference between means of St. Lawrence region and Maine significant. $P < .001$

Difference between means of Kent I. in 1947 and Kent I. in 1948 insignificant.

Difference between means of St. Lawrence region in 1936 and St. Lawrence region in 1938 insignificant.

TABLE III. *Greatest number of eggs present in nests producing young and in nests failing to produce young*

Clutch-size	Nests producing young		Nests not producing young	
	No. of nests	No. of eggs	No. of nests	No. of eggs
1	1	1	2	2
2	6	12	18	36
3	11	33	26	78
4	14	56	31	124
5	5	25	12	60
6	2	12	4	24
7	0	0	1	7
8	0	0	1	8
Total	39	123	95	339
Mean	3.56 $\pm$.18		3.57 $\pm$.12	

puted for only the 39 nests that produced young (Table III). This gave a mean of $3.56 \pm .18$. Then the mean clutch was computed for the 95 nests that did not produce young, giving a mean of $3.57 \pm .12$. The difference between the two means hardly needs statistical treatment to prove it to be insignificant. In other words, it appears that few, if any, nests with incomplete clutches were included in the 95 nests that did not produce young. From this test we may also assume that there is no difference in the clutch-size of nests that produce young and those that do not, unless, of course, larger clutches are found in unsuccessful nests but this possibility is obscured by the inclusion of a number of incomplete clutches in the sample. However, owing to the difficulties in locating nests before incubation has begun, probably few nests with

incomplete clutches were found and most of these produced full clutches before being destroyed.

There are available few data on the mean clutch-size at Kent Island in other years. In 1932 Gross (1938) found that "The average number in one hundred nests of complete sets was 4.4 eggs per nest." This mean is probably too high since only "complete" nests were censused and a certain amount of bias presumably entered the sampling, causing smaller clutches to be disregarded, since they were considered to be incomplete.

On June 12, 1947, I counted the eggs in 28 nests (Table II) on Kent Island and found the mean clutch to be $3.36 \pm .28$. Presumably, because of the date of the census, few incomplete clutches were included in the sample, although nests may have lost eggs through predation. The difference between the mean clutch in 1947 and that of 1948 is statistically insignificant (see Simpson and Roe (1939) for statistical treatment), and it may be assumed that the mean clutch-size was essentially the same in 1947 and 1948.

As Lack (1947, 1948) has pointed out, in many double-brooded birds the mean clutch-size increases from early spring to about June and then declines. However, among single-brooded birds, which are mostly non-passerine, there seems to be no difference in the size of clutches throughout the breeding season, unless the nest is robbed. In that case, repeat layings show a decline in the mean number of eggs. Lack (1947) has given a list of normally single-brooded species which

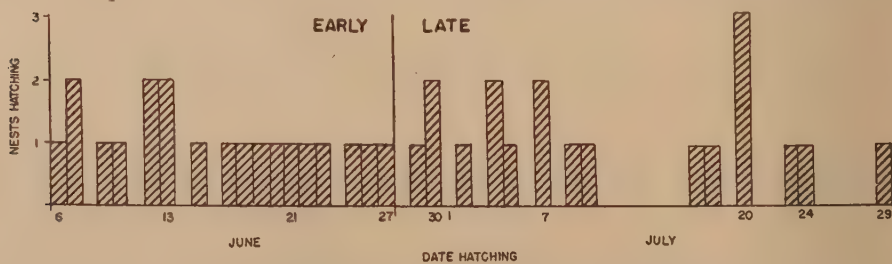


FIG. 3. Dates of hatching for 39 nests that produced young.

exhibit repeat layings and quotes Koenig and Le Roi (1911), who found that the European eider (*Somateria m. mollissima*) in Spitsbergen lays between 4 and 6 eggs at its first laying and 3 to 4 eggs at repeat layings.

Because, in the majority of cases, the date of the completion of the clutches at Kent Island is unknown, the determination of early and late nesting birds must be based on the hatching dates. This reduces the available data to the 39 nests which produced young in 1948.

Dates of hatching have been plotted in Figure 3. The hatchings were rather equally distributed over a span of 54 days, but rather than divide the nests into early and late groups on a time basis, which would yield more unequal samples, the first 20 nests to hatch have been called "early" and the remaining 19 nests "late." That is, nests hatching between June 6 and June 27 are early nests and those hatching between June 28 and July 29 are late nests. Unfortunately, it is unknown whether or not any of the late nests represent repeat layings. Contrary to Koenig and Le Roi (1911), I am inclined to believe that the eider, at least *S. m. dresseri*, seldom lays a second clutch if the first is destroyed, since the males begin to desert the shores of the island in mid-June and congregate on isolated ledges, a considerable distance from land, where they undergo a post-nuptial moult. It is possible, however, that the few males which remain until early July mate with birds which re-nest, as well as with those which nest for the first time late in the season. This is a difficult problem to investigate.

It may be seen from Table IV that the mean clutch-size for early nests was $3.80 \pm .28$, whereas late nests had a mean of $3.32 \pm .20$. The difference between the means is statistically insignificant, although the modes are somewhat different, and it may be concluded that, at least in *S. m. dresseri*, there is probably no difference between the clutch-size of early and late nesters, even if some of the late nests represent second layings, which is doubtful.

TABLE IV. *Clutch-size of early and late nests*

Clutch-size	Early nests (hatching June 6-27)		Late nests (hatching June 28-July 29)	
	No. of nests	No. of eggs	No. of nests	No. of eggs
1	0	0	1	1
2	4	8	2	4
3	5	15	6	18
4	4	16	10	40
5	5	25	0	0
6	2	12	0	0
Total	20	76	19	63
Mean	$3.80 \pm .28$		$3.32 \pm .20$	

Difference between means insignificant.

SURVIVAL OF THE EGGS

Of the 134 nests considered in the study, only 39 or about 29 per cent produced young. These 39 nests hatched a total of 123 young, or an average of 3.15 birds per nest. Looking at it in a different light, the 134 nests in the entire study produced only an average of slightly more than 0.9 birds per nest, an impressively low rate of reproduction. All eggs were lost through predation. None was infertile or failed to hatch.

The loss of eggs at Kent Island is caused, almost exclusively, by herring gulls although crows (*Corvus b. brachyrhynchos*) and ravens (*Corvus corax principalis*) may account for some losses. Many times I have observed a gull discover an eider nest and begin to eat the eggs. In most cases, other gulls are quick to discover the unguarded eggs and the nest and its contents are soon destroyed by a mass of fighting birds. The eider duck is unattended by the male, and when she leaves the nest to feed in the water for a short while, or is frightened away, the eggs are unprotected. Consequently, all the eggs are usually destroyed at once rather than one or two at a time, as is the case with gulls where predators are usually discovered and driven off by the guarding bird.

As in all studies of this type, the presence of the observer is probably a factor

contributing toward lower survival rates than normal, although this is impossible to evaluate. With the eider, disturbance by the observer may be particularly important, since the ducks do not stay near the nest ready to resume incubation, as do gulls, but fly off and spend some time in the water until the gulls have settled down and the colony regains its usual character. Although I saw few study nests destroyed by gulls, I believe the mortality rate was definitely increased owing to my presence.

Evidence from the herring gull (Paynter 1949) has indicated that the survival rate of eggs is better in nests which contain close to the mean number of eggs for the species than in nests with fewer eggs. Evidence from larger clutches is lacking. It was suggested that increased visual or tactile stimulation causes the adult to give better care to the eggs. In the Alpine swift (*Apus melpa*) (Lack and Arn 1947), however, clutch-size is not related to survival rate, but this is not unexpected, since the eggs suffer little from predation because of the more or less concealed nests.

To test for variations in survival rates of eggs in the eider, Table V has been drawn up. Applying the chi-square test (Fisher 1941) for the significance of the difference in frequencies of predation on various clutch-sizes in the entire group

TABLE V. *Clutch-size as related to survival rates of eggs*

Clutch-size	All 134 nests in study		39 nests producing young	
	No. nests	No. nests suffering loss of any eggs	No. nests	No. nests suffering loss of any eggs
1	3	2	1	0
2	24	18	6	0
3	37	29	11	3
4	45	39	14	8
5	17	12	5	0
6	6	4	2	0
7	1	1	0	0
8	1	1	0	0
Total	134	106	39	11
Percentage suffering loss	79.11		28.20	

TABLE VI. *Hatching success of early and late nests*

Clutch-size at hatching	Early nests (June 6-27)		Late nests (June 28-July 29)	
	No. of nests	No. of eggs	No. of nests	No. of eggs
1	3	3	1	1
2	4	8	4	8
3	4	12	10	30
4	2	8	4	16
5	5	25	0	0
6	2	12	0	0
Total	20	68	19	55
Mean	3.40 ± .37		2.89 ± .19	

Difference between means insignificant.

of 134 nests, it was found that the differences are not significant or, in other words, clutch-size does not seem to be related to survival rate. However, it should be borne in mind that most nests were not found until after incubation had begun. Consequently, although we know predation is equally severe upon all clutch-sizes after incubation has started, we do not know whether predation rates differ before incubation begins and while the eggs are unprotected. When the survival rate is considered only for the eggs in nests which produced young (Table V), a chi-square test indicates ($P < .02 > .01$) that 3- and 4-egg nests suffer from predation more than smaller or larger clutches. Nevertheless, because the clutches are not equally distributed in the sample, predation by gulls in a random manner would naturally occur more often in 3- and 4-egg nests than in clutches of other sizes. It is interesting to note that of the 11 nests which produced young and suffered from predation, 10 lost only one egg each and the other, a four-egg nest, lost 3 eggs.

Although no significant difference in clutch-size between early and late nests has been found, it was thought of interest to test for variations in the number of young produced during the season. Again dividing the nests into early and late groups, as in Table IV, it was found (Table VI) that $3.40 \pm .37$ young were produced per nest in the early series and

$2.98 \pm .18$ young in the late nests. The difference is insignificant. It may be concluded that early nests and late nests are equally successful in producing young, and predation pressure does not seem to vary appreciably throughout the season.

DISCUSSION

In his recent outstanding work on the significance of clutch-size, Lack (1947, 1948) has reported many cases, particularly in the passerines, in which the mean clutch-size of a given species increases from south to north. This Lack attributes to longer periods of daylight during the breeding season in the north. The suggestion that the longer food-gathering time permits larger broods to be raised seems to be well founded, at least for those passerine birds that show geographical variation of clutch-size. However, among gannets, petrels, doves, shore birds, and others (see Lack (1947) for complete list), geographical trends are apparently absent. There are few clutch-size data available for ducks, and Lack was unable to arrive at a satisfactory conclusion regarding them. He found that *Somateria m. mollissima* normally lays 4 to 6 eggs in Britain, whereas Jourdain (1922) reported the usual clutch in Spitsbergen to be 6 to 7 eggs. This seemed to indicate a south to north trend, but Koenig and Le Roi's data (1911) indicated the clutch-size in Spitsbergen to be only 4 to 6, as in Britain. Obviously, with such contradictory evidence, little can be done with the European race of eider at this time. In eastern North America the data are also few, but nevertheless better, and a clear-cut case of a geographical trend is found. These data have been presented in Table II.

On June 7, 1933, Gross (1938) censused all the nests he found in the Penobscot Bay region of Maine, regardless of whether he thought them to be complete or not, and obtained a mean of $3.25 \pm .10$. The nesting season was well advanced at this period and probably few nests contained incomplete clutches. Al-

though the difference between the means in Maine in 1933 and Kent Island in 1947 is not statistically significant, when the mean is computed for Kent Island for 1947 and 1948 combined ($3.53 \pm .09$) and this is compared with the mean for Maine, a significant difference is found.

As might be expected, since the distance between Kent Island and the north shore of the Gulf of St. Lawrence is considerably greater than the distance between Kent Island and Penobscot Bay, the variation between the mean clutch at Kent Island and that of the St. Lawrence region is much more pronounced.

Lewis (1939) counted the number of eggs in 1,131 eider nests, during the breeding season of 1934 through 1938, and found the mean clutch-size for the entire period was $4.04 \pm .03$ eggs per nest. This is significantly different from the Kent Island figure. Although the periods of observation varied from year to year and the samples were unequal, it is interesting to note that in not one year did a mean in the St. Lawrence region overlap that of Kent Island. It should also be noted that the means obtained by Lewis are probably somewhat lower than the true figures, since no nests were observed for more than a day and some of the nests censused early in the season may not have had complete clutches, while other nests may have lost eggs through predation.

Examination of the data obtained by Lewis in 1936 and 1938 shows some peculiar features. In 1936 the clutch-sizes were not equally distributed in the sample but were abruptly terminated at five eggs, causing the clutch-size to drop to $3.89 \pm .30$, the lowest mean recorded in the five-year study. It is possible that the small size of the sample may have caused this anomalous distribution. In 1938, although the census began earlier than usual and probably included more incomplete clutches, the mode shifted for the first time from 4- to 5-egg clutches. This resulted in a mean of $4.25 \pm .07$, the highest obtained during the study, but the difference between the highest

and the lowest means is not statistically significant.

In view of the fact that Maine once again represents the southernmost breeding area of the eider, it is possible that most of the present breeding population there has been derived from the northern populations. Since the birds in the north have been shown to lay significantly larger clutches than those in the south, it would seem that a reduction in clutch-size may not be an inherited character but rather a physiological condition easily and rapidly adjustable to geographical changes in breeding areas. It would be interesting to test this hypothesis by breeding northern birds in the southern part of the range.

The causative mechanisms which determine clutch-size in the Anatidae are not easy to discover, and the reasons for the geographical variations are even more obscure. Most ducks do not feed their young but merely protect them while they hunt for their own food in the water. Obviously, if each duckling fends for itself, there is no feeding problem for the adult, no matter how large her brood may be. Thus, food provided by the adult cannot be a factor limiting clutch-size in ducks.

If the young are subject to predation, there must be an upper limit to the number of young in a brood which an adult can protect. It hardly seems possible, though, that this limit should be so rigidly defined by severe selection, that an adult can only care for 3 or 4 young and one or two additional ducklings are so detrimental that the whole brood suffers. Rather, one would expect that the excess young would simply be killed off, and the adult would then be able to protect the remaining young. For example, if 4 young in a brood were the optimum number, adults with 8 ducklings would raise the same number of young as an adult with 4 young. There would be no disadvantage in larger broods once the excess young had been killed. Also, in many ducks, including the eider, broods are

frequently amalgamated, and a raft of 20 young is protected by 5 or 6 adults. It is difficult to imagine how predation could select for brood-sizes in cases such as this, for unless the entire brood suffered equally, selection could not act. Thus, limitation on brood size does not seem likely to be a factor limiting clutch-size in most Anatidae.

Lack (1947) suggested that because a duck does not incubate during the laying period and the eggs are unprotected during that time, theoretically, a shortening of the laying period would be advantageous in that it would reduce the possibility of predation. The easiest way to shorten the laying period would be to reduce the clutch-size. Lack calculated that a loss of about 17 per cent per day would be necessary in order to make a reduction from 6 to 5 eggs advantageous to the eider but, as he concluded, this seems to be an absurdly high figure. Evidence from Kent Island showing that clutch-size is not related to egg survival would seem to dispel this theory. However, it should be remembered that very few incomplete clutches were included in the study, and what has been shown is that once incubation has begun, all clutches have equally good chances of hatching. It is possible that larger clutches, which, of course, require longer laying periods, were destroyed during the laying period and did not enter the study. Nevertheless, a rate of loss of 17 per cent per day seems exceedingly high, even at Kent Island where there is such a large concentration of gulls, and while a shortening of the laying period is theoretically advantageous where predation pressure is great, it has yet to be proved in the field. We must admit then that the cause, or causes, determining clutch-size in the Anatidae are still unknown.

While it is difficult to speculate on the causes of geographical variations in clutch-size among the eiders of eastern North America, when the causes which determine clutch-size in the species as a whole are not understood, it is possible

that the increase in the periods of daylight in the north may play some part, although not through increased food-gathering time, as Lack has found in other birds. Greater periods of daylight would provide more time for predation. If predation occurs in a random manner in all clutch-sizes, larger clutches would be necessary to compensate for those nests which were lost. For example, if 10 nests had 4 eggs each and 50 per cent of the nests were destroyed, only 20 young would be produced. But if the 10 nests had 6 eggs each and predation occurred at the same rate, 30 young would be produced. Eventually, birds which are inherently layers of larger clutches would be a major part of the population. Of course, there are no data to support this hypothesis, and it is in conflict with the suggestion previously made, that clutch-size in the eider is not genetically determined, but it seems to be a reasonable explanation of a difficult problem.

SUMMARY

1. The mean clutch-size at Kent Island is $3.53 \pm .09$; there is no significant difference between the mean of 1947 ($3.36 \pm .28$) and the mean of 1948 ($3.56 \pm .10$).
2. There is no difference between the mean clutch-size of nests that produce young and of those that do not.
3. There is no significant difference between the clutch-size of early nests ($3.80 \pm .28$) and of late nests ($3.32 \pm .20$).
4. Twenty-nine per cent of the nests studied produced young; 3.15 birds were produced per nest in the 39 nests hatching young or only 0.9 birds per nest for the entire group of 134 nests. Human disturbance may have contributed toward a high mortality rate.
5. Clutch-size is not related to survival rates, at least after incubation has begun.
6. Early nests and late nests are equally successful in producing young.
7. A geographical trend in clutch-size

has been found. The mean clutch-size in Penobscot Bay, Maine is $3.25 \pm .10$, at Kent Island, New Brunswick it is $3.53 \pm .09$, and on the north shore of the Gulf of St. Lawrence it is $4.04 \pm .03$.

8. The causes determining clutch-size for the species as a whole are unknown. It has been suggested that geographical variations may be related to the increased periods of daylight in the north. More daylight hours would provide more time for predation and larger clutches would be necessary to offset the greater loss of nests.

LITERATURE CITED

- Brownson, W. H.** 1908. A visit to Grand Manan Island. *Jour. Maine Ornith. Soc.*, 10: 72-77.
- Fisher, R. A.** 1941. Statistical methods for research workers. 8th Edition. xv + 344 pp. Edinburgh: Oliver and Boyd.
- Gross, A. O.** 1938. Eider ducks of Kent's Island. *Auk*, 55: 387-400.
- . 1940. The migration of Kent Island herring gulls. *Bird-Banding*, 11: 129-155.
- . 1944. The present status of the American eider on the Maine coast. *Wilson Bull.*, 56: 15-26.
- Jourdain, F. C. R.** 1922. The birds of Spitsbergen and Bear Island. *Ibis*, 1922: 159-179.
- Koenig, A., and O. Le Roi.** 1911. Avifauna Spitsbergensis. x + 294 pp. Bonn.
- Lack, D.** 1947. The significance of clutch-size. *Ibis*, 1947: 302-352.
- . 1948. The significance of clutch-size. *Ibis*, 1948: 25-45.
- , and **H. Arn.** 1947. Die Bedeutung der Gelegenheitsgrösse beim Alpengregler. *Der Ornithologische Beobachter*, 44: 188-210.
- Lewis, G. F.** 1939. Size of sets of eggs of the American eider. *Journ. Wildlife Manag.*, 3: 70-73.
- Norton, A. H., and R. P. Allen.** 1931. Breeding of the great black-backed gull and double-crested cormorant in Maine. *Auk*, 48: 589-592.
- Paynter, R. A., Jr.** 1947. The fate of Kent Island herring gulls. *Bird-Banding*, 18: 156-170.
- . 1949. Clutch-size and the egg and chick mortality of Kent Island herring gulls. *Ecology*, 30: 146-166.
- Pettingill, O. S., Jr.** 1939. The bird life of the Grand Manan Archipelago. *Proc. Nova Scotian Inst. Sci.*, 19: 293-372.
- Simpson, G., and A. Roe.** 1939. Quantitative zoology. xvii + 414 pp. New York: McGraw-Hill.

VEGETATION MAPPING AS A GUIDE TO BETTER SILVICULTURE

MARINUS WESTVELD

*Northeastern Forest Experiment Station, Forest Service,
U. S. Department of Agriculture*

INTRODUCTION

Difficult and challenging problems confront the forester today. Disastrous floods, critical water shortages, and the uninterrupted trend of forest depletion have focused attention on the important role forests play in the strength, economy, and prosperity of the Nation. Forests are increasingly prized for recreation, the protection they afford sources of water, and beneficial effects on stream flow and erosion. These factors contribute much to the health and well-being of the public; hence they should receive full consideration in the shaping of forest policy and management objectives.

The forester faces the very real problem of managing the forest resources at a profit and accomplishing this without injury to the productive powers and protective values of the soil and forest. This is a large order. It is tantamount to eating your cake and having it too.

Too often forestry is treated simply as an economic and engineering problem. When it is, cutting operations leave large areas exposed to wind and water. Soil porosity is decreased; recreational and other basic forest values are seriously impaired; the very elements that give forests their value are destroyed. Under such mismanagement, stand composition and quality deteriorate, and the forest becomes easy prey to a host of insects and diseases.

The spruce-fir forests are a good case in point. Continued clear-cutting of these forests has not only reduced their watershed-protection value, timber yield and quality; it has also greatly increased their susceptibility to insect attack. Clear-cutting has greatly increased the proportion of balsam fir, the favored

host of the destructive spruce budworm. Witness also the rapid spread of birch die-back and beech scale with its accompanying *Nectria* canker in our northeastern hardwood forests. These pests have their origins in the consistent creaming of the forest for the best trees, leaving extensive areas dominated by cull and weakened trees—conditions ideal for the outbreak of native and introduced forest pests.

ECOLOGY THE BASIS FOR SOUND SILVICULTURE

How can we control the destructive agents that threaten to curtail and impair the usefulness of the forests? How can we promote and maintain conditions favorable to multiple use with a minimum of detriment to the forest?

The answer lies in the application of sound silviculture, silviculture based upon biological facts and principles. Intelligent management of our forests cannot be achieved without thorough knowledge of the behavior of tree species and stands. Foresters must know how specific forest types react to the various habitat factors if serious errors in silviculture are to be avoided.

Nature, unguided by man, produces a forest that is in complete harmony with the soil and the plant and animal life it supports. Such a forest is the climax forest toward which vegetation is always tending. Stable tree associations, characteristic of climax types, are best adjusted to meet the impact of antagonistic forces. Such forests are inherently healthy; under good management they are easily maintained in a high state of vigor, thus increasing their capacity to resist damage from insects, disease, and other destructive agents.

For every tree species or group of species, there is an optimum site. To try to grow species ill adapted to the site is but an open invitation to inroads by damaging pests. Nature vigorously protests against violation of her laws; disregarding them can lead only to serious trouble.

Numerous examples of such violations can be cited. Nectria canker occurs in certain northern hardwood stands in New England because they occupy sites that were originally in possession of pure softwoods or softwood-hardwood mixtures. Persistent cutting of softwoods only—and subsequent fires—made possible the complete occupation of these sites by northern hardwoods despite site factors adverse to their satisfactory development. To control this troublesome disease, foresters face the difficult task of reconverting these sites to their original composition. To attempt to maintain northern hardwoods on such sites is foolhardy. Another example is the damage the Tympanis canker and the European pine shoot moth are inflicting on red pine planted south of its natural range.

There is much to indicate that the more closely the forester adapts his silvicultural practices to the natural laws operating in a given site, the more simple become his problems of timber production. This is not meant to imply that the climax forest type necessarily represents the ideal toward which management should invariably be directed. In the Northeast, for example, fires, repeated cuttings, and other disturbances have so altered soil conditions that early establishment of species natural to the site may be difficult or even inadvisable. The impact of introduced foreign pests may force us to strive for compositions different from those that characterized the original site. Moreover, the high value of certain subclimax species such as Douglas-fir, black cherry, and white pine may justify efforts to maintain them as dominants in the stand. Nevertheless, compositions characteristic of climax associations should be used as guides for

setting up silvicultural objectives. Such an approach is basically sound. Such silviculture will greatly expedite the attainment of the multi-purpose goals of forest management.

MAPPING FOREST VEGETATION

Since climax forests provide the key to successful forest management, the first step in a program for placing the silviculture of a region on a firm basis is the classification of its forests into natural forest types. Such an undertaking in the Northeast is not easily accomplished. Opportunity for presenting a truly accurate picture of its original forest cover disappeared more than 200 years ago. Today much of the Northeast's forest cover is a hodge-podge of temporary types in varying stages of succession. This, however, need not deter attempts to reconstruct the climax forest associations of the region. Schemes for accomplishing this will be discussed in this paper.

In the past, men like Shantz, Zon, Clements, and others have taken a leading role in classifying and mapping the major units of vegetation in the United States. But these classifications are too broad and general in character to meet the needs of the average forester. To be of real value to a forester, type maps should be on a relatively large scale. More informative are the forest-type maps currently being made by the U. S. Forest Service in conjunction with its survey of the Nation's timber resources.

Such a survey is at present in progress in the Northeast. The latest techniques of aerial-photo interpretation are employed for determining timber volume and type and stand boundaries. With the aid of stereoscopes and checking on the ground, skilled interpreters can delineate forest types from aerial photos—with surprising speed and accuracy. This is particularly true with photos taken in the fall when leaves are in the process of coloring. Such photos afford maximum contrasts in shading, thus

greatly facilitating identification of forest types and tree species.

But it should be borne in mind that type mapping of the sort conducted by the U. S. Forest Service is concerned primarily with the quantity and quality of the present timber crop. The basis for type classification is more one of economics than ecology. The intrinsic value of the tree species now making up the stands, and their potentialities as an industrial resource, are the controlling factors. The species or species group that constitutes 50 per cent or more of the timber stand determines the type designation. Under this scheme existing tree cover, irrespective of its ultimate development, provides the basis for type classification.

Such a classification is purely utilitarian, but justifiably so. Should the types have an ecological equivalent, this is wholly coincidental. Thus, it often occurs that sites radically different ecologically from one another nevertheless receive uniform type designations simply

because the predominating species or species groups are currently the same. On the other hand, an ecologically uniform site may be divided into several cover types because of variation in stand composition occurring within the unit. In basic site classification, boundaries are stable.

DETERMINING CLIMAX TYPE FROM CURRENT FOREST COVER

Where the forests have undergone only minor modifications, cover-type maps may still provide the clue to the climax type. But in the Northeast, where forest disturbances have been rampant and radical, the original forest over extensive areas has undergone profound changes. For example, pure stands of old-field spruce and pine now occupy soils that prior to cultivation supported fine stands of hardwoods. On the other hand, years of cutting for spruce and fir only in mixed spruce-hardwood stands have converted extensive areas to pure hardwoods. Elsewhere forests of pin cherry, mountain

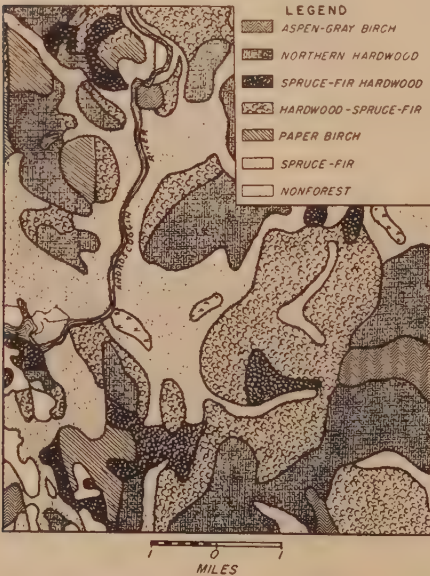


FIG. 1. Present forest cover types in a portion of the Milan, New Hampshire, quadrangle.

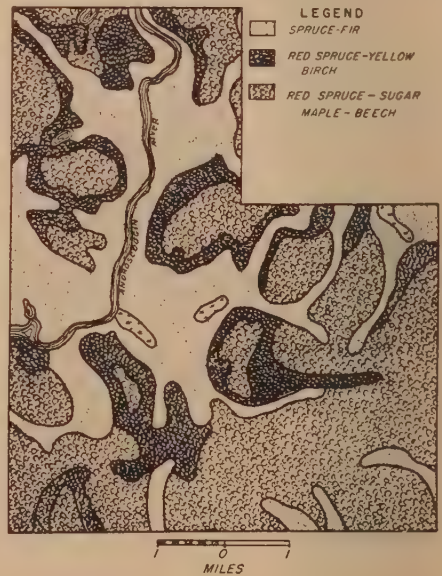


FIG. 2. Climax associations of the same area (Fig. 1), as interpreted from present cover types.

maple, aspen, and paper birch have taken possession of the land in the wake of heavy cutting, fires, and insect epidemics.

To interpret each and every temporary type variant in terms of climax associations calls for more knowledge about forest-type succession than has been gathered to date in the Northeast. However, as our fund of knowledge on forest succession increases, interpretation of temporary cover-types into climax associations can be undertaken with increased confidence. Illustrative of such an attempt are the two maps shown for portions of the Milan quadrangle in northern New Hampshire. Figure 1 is the cover-type map prepared by the Forest Survey unit of the Northeastern Forest Experiment Station. Figure 2 is an interpretation of these types into climax associations.

DETERMINING CLIMAX TYPE THROUGH SITE-TYPE CLASSIFICATION

If cover-type maps solve only part of the problem of reconstructing the natural forests, what other recourse is there?

Cajander's (1926) site-type classification, in which indicator plants are used to identify site, presents one possibility. This system is based upon the thesis that specific plants (indicator plants) forming a part of the minor vegetation in the forest are associated with soil quality and natural succession. This concept recognizes that vegetative communities constitute distinct entities developed and arranged in accordance with definite biological laws and are not mere aggregations of plants brought together by chance. Such plant associations are well differentiated and are very constant for the same site type. Even though the stand is subjected to disturbance, the ground vegetation quickly comes back into equilibrium. A plant community is an excellent indicator of site, for it is the integration of all the factors that govern growth. Through this principle, it is possible to develop a classification of ground-vegetation types that are indica-

tive of site-quality classes. From these, sites can be identified in terms of natural forest types.

Each plant association is characterized by one or several plants that are biologically dominant. It is true that a specific plant species may be common to several associations, but in one of them it is harder and better able to withstand competition than its associates. It is this that provides the key to the recognition of various plant associations. It should not be assumed, however, that plant communities can always be recognized at a glance. One needs training and experience to be able to classify them correctly.

It is important to remember that in basic type delineation we are dealing with site factors that are presumed to obtain under climax conditions. It should not be inferred from this, however, that appraisal of existing site factors can be ignored, particularly those factors that enjoy a certain degree of stability. Slope, elevation, aspect, drainage, soil texture, soil depth and pH value are all of primary importance and should be kept in the foreground. The form and vigor of plant communities faithfully reflect the over-all effects of these factors. Although based on present conditions, they do provide a ready index for site-type determination.

DEVELOPMENT OF SITE-TYPE CLASSIFICATION IN THE NORTHEAST

In the Northeast, considerable progress already has been made in defining the various forest types floristically. The Northeastern Station began detailed studies of the minor vegetation in the spruce-fir and northern hardwood types as early as 1924.¹ Other agencies followed with similar studies elsewhere in the region. Interest was stimulated further by the Finnish forester Ilvessalo

¹ These studies were based on milacre transects established in the major forest types of the spruce-fir and northern hardwood region. On each quadrant the frequency and comparative area in possession of each ground-cover species encountered was determined.

TABLE I. Tentative forest-type—site-type classifications for spruce-fir and northern hardwood region of the Northeast

Forest type	Society American Foresters type number	Topographic position	Minor-vegetation type*	Characteristic humus type	Ultimate forest-type group	Species to favor
Black spruce	23	Swamp	Sphagnum-Ledum	Peat or bog-like formation	Softwoods	{ Black spruce Red spruce Balsam fir
Red spruce	18	High slope	Oxalis-Hylocomium	Mainly greasy mor		
Balsam fir	22	Flat	Hylocomium-Hypnum Cornus-Maianthemum	Mainly felty mor		
Red spruce	18	Flat	Hylocomium-Hypnum Cornus-Maianthemum	Mainly felty mor		
Paper birch-red spruce-balsam fir	20	Upland flat	Cornus-Maianthemum	Greasy or felty mor	Mixed wood	{ Red spruce Balsam fir Yellow birch Paper birch
Red spruce-yellow birch	16	Bench-gentle slope	Oxalis-Cornus	Greasy or felty mor		
Red spruce (old field)	18	Bench	Oxalis-Cornus	Old-field mor		
Red spruce-sugar maple-beech	17	Lower slope	Viburnum-Oxalis	Granular mor		
Red spruce (old field)	18	Well-drained sites	Viburnum-Oxalis	Old-field mor	Hardwoods	{ Sugar maple Yellow birch Red spruce White ash Black cherry Basswood
Yellow birch	15	Lower slope and benches	Viburnum-Lycopodium Viburnum	Granular mor and fine mull		
Sugar maple-beech yellow birch	12	Low ridges, gentle slopes, deep soils	Viburnum-Taxus Oakesia-Maianthemum	Fine and medium mull		
Sugar maple	14	Coves, well-drained sites	Arisaema	Medium and coarse mull		

* *Sphagnum* spp., sphagnum moss; *Ledum groenlandicum*, Labrador tea; *Oxalis acetosella*, wood sorrel; *Hylocomium splendens*, feather moss; *Hypnum cristata-castrensis*, feather moss; *Cornus canadensis*, bunchberry; *Mainithemum canadense*, Canada mayflower; *Viburnum alnifolium*, witch hobble; *Lycopodium lucidulum*, shiny clubmoss; *Ilex canadensis*, ground huckleberry; *Oakesia sessilifolia*, oakesia; *Arisaema triphyllum*, jack-in-the-pulpit. Scientific nomenclature follows Gray's Manual, seventh edition, 1908, for flowering plants, and Grout's Mosses with a hand lens, 1924, for mosses.

(1929) following his site-type classification work in Canada and the United States in 1927. Of particular note is Heimburger's (1934) work in the Adirondack region. In recent years the Dominion Forest Service and other Canadian research agencies have contributed liberally to the literature on site-type classification (Holman 1929, Brunkman 1936, Sisam 1938, Linteau 1940, Ray 1941).

A tentative forest-type—site-type classification for the spruce-fir and northern hardwood forests of western Maine, New Hampshire, Vermont, and the Adirondacks is presented in Table I. This classification is to a large degree based on the systematic studies of forest stands and minor vegetation conducted by the above-mentioned workers and agencies. The major forest and minor vegetation types and other features such as soil, drainage, and humus formations (Heiberg 1941) that help to identify them are also listed.

APPLICATION OF THE SITE-TYPE THEORY TO SPRUCE-FIR—NORTHERN HARDWOOD REGION

It is pertinent at this stage to discuss briefly the potential value of floristic-type mapping as a guide to better silviculture. This can be done effectively by illustrating its application to a group of forest types common to the northeastern forests.

It will be seen (Table I) that the spruce fir-northern hardwood forests have been divided into three classes: (1) predominantly softwoods, (2) varying mixtures of softwoods and hardwoods, and (3) predominantly hardwoods. Within these broad groups 12 forest types are now recognized (Society of American Foresters, 1932). Opposite each forest type is listed one or more ground-vegetation types. The ground-vegetation types here set up are arranged on a scale of ascending soil fertility. Thus each forest type is assigned its proper niche in the site-quality scale, as

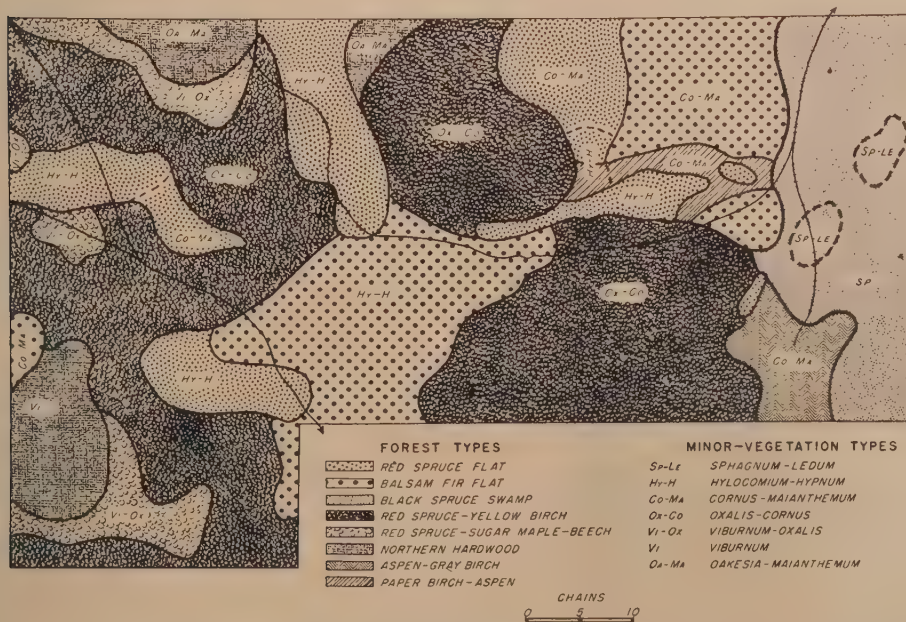


FIG. 3. Relationship between forest type and ground-vegetation type on a portion of the Gale River Experimental Forest, Grafton County, New Hampshire.

well as its ground-vegetation type equivalent.

For some forest types, two ground-vegetation types are listed. In such instances it may be assumed that at least two ecological types of different fertility levels comprise the forest type.

A ground-vegetation-type map is the practical equivalent of a type management map. Therein lies its real value, for ground-vegetation types can be translated directly into site potentialities. Thus they serve to identify the true forest characteristics of the site even though these have become masked. A map of a segment of the Gale River Experimental Forest in northern New Hampshire shown in Figure 3 illustrates the relationship existing between forest types and ground-vegetation types. It is of interest to note that four forest types have a minor vegetation type (*Cornus-Maianthemum*) common to them all. It may be assumed that these forest types constitute one biological entity and currently represent transitional stages in a successional series which if left undisturbed would ultimately attain a common climax (spruce-fir).² On the other hand, elsewhere on the map appear forest types containing more than one vegetation type. These are illustrations of forest types embracing two ecological entities of different fertility levels. Since correct site appraisal is the key to sound silviculture, ground-vegetation-type maps can be used as guides for proper orientation of silvicultural goals. Once the property has been classified into sites, the problem of setting up correct

silvicultural goals and attaining the full productive capacity of the soil is made infinitely easier.

Let us consider for a moment the significance of this concept in terms of the forest types listed in the table. The ground-vegetation type equivalent of the red spruce-yellow birch type, for example, is *Oxalis-Cornus*. Even should the present tree cover, owing to the past cutting practices, consist mainly of hardwoods, the presence of *Oxalis acetosella* and *Cornus canadensis*, key indicators of softwood sites when they occur in combination, warns the forester against managing primarily for hardwoods. Here silviculture should be aimed at reestablishing the normal softwood representation. This is further indicated by the presence of abundant advance spruce-fir reproduction (Recknagel 1933).

On these sites, particularly where some *Viburnum alnifolium* comprises part of the ground vegetation, yellow birch attains good development as well as spruce and fir. Management for a red spruce-yellow birch association appears fully justified silviculturally. On the best soils of the *Viburnum-Oxalis* type, sugar maple is a legitimate objective, in addition to yellow birch. This is indicated by the preponderance of hardwood over conifer reproduction on these sites (Recknagel 1933). On the *Sphagnum-Ledum*, *Oxalis-Hylocomium*, and *Hylocomium-Hypnum* sites, the only logical and practical goal is softwood production.

On the other hand, to strive for spruce-fir dominance in the various *Viburnum* associations and the *Oakesia-Maianthemum* and *Arisaema* associations can lead only to

² The place in succession of the forest types depicted on the map are judged to be as follows:

Type name

Red spruce flat
Balsam fir flat
Black spruce swamp
Red spruce-yellow birch
Red spruce-sugar maple-beech
Northern hardwoods
Aspen-gray birch
Paper birch-aspen

Place in succession

A climax—spruce-fir
Subclimax to spruce-fir
A climax
A probable climax
A climax
A climax
A pioneer type followed eventually by spruce-fir
A pioneer type followed eventually by spruce-fir

disappointment. The deep, fertile soils characteristic of these sites strongly favor hardwoods. Under the keen competition these hardwoods exert, red spruce has little opportunity of becoming established, except through costly cultural measures. Here management should be directed to the production of high-quality hardwoods. This is indicated by the presence of such herbaceous plants as *Oakesia sessilifolia*, *Arisaema triphyllum*, *Impatiens biflora*, and *Laportea canadensis*, and such shrubby growth as *Viburnum alnifolium*, *Cornus alternifolia*, and *Ribes cynosbati*.

TECHNIQUES OF SITE-TYPE MAPPING

What are the possibilities of recognizing and mapping site type through aerial photo interpretation? Aerial photos are being successfully employed in cover-type mapping even to the extent of delineating stands into height, density, and condition classes. Where the forests still occur in their natural state, site-type delineation is an almost routine job of aerial photo interpretation, since climax forests directly express site quality.

But where the true character of the forest has become obscured and plant indicators are substituted as indices for site-type, the problem becomes more complex because ground vegetation cannot be identified on aerial photographs. Such identification can be greatly aided, however, through cross-classification of related factors. Certain basic factors visible on the photos and subject to appraisal are important in the determination of site.

Topography, for example, is one site factor that can readily be recognized on aerial photographs. Topography, in turn, strongly influences the character of the soil, a second important site factor. Stereoscopic study of topography in terms of aspect, location, elevation, and degree of slope provide excellent leads on broad soil groups. The experience of Moesner (1948), Hills (1950), and others indicates that skilled interpreters can readily classify forest areas into sites based on topo-

graphic position and soil groups. Losee (1942), in his attempts to map site-types from aerial photos, found that these soil patterns corresponded reasonably well with ground-vegetation types. This is not surprising: the site-type theory is essentially based on soil classification, indicator plants serving as indices of soil quality.

A skilled photo interpreter who can recognize site relationships, if further fortified by first-hand knowledge of the region and a thorough understanding of forest types and the significance of key tree species, should be able to prepare a site-type map that satisfactorily expresses the capabilities of the land for forest production. Within such broad basic sites, however, are likely to occur not one, but several different plant associations. Such a site-type map may well be a disappointment to those who insist that ground-vegetative types are the acme of site-type classification. Where a further breakdown is needed to bring out important site differences, these broad groupings provide a convenient framework.

If aerial photo analyses fail to provide the degree of site-type refinement needed for management purposes, it will be necessary to resort to ground mapping. Where ground-vegetation-type mapping is the objective, the techniques employed in regular forest-type mapping will be found adequate. In fact, the mapping should, if possible, be conducted in conjunction with the regular forest survey by assigning to the survey crew a skilled vegetation mapper. This makes for greater economy and accuracy.

Mapping can best be accomplished through the standardized system of parallel traverse lines at sufficient frequency to cover all variations in vegetation. At regular intervals along these lines, the mapper determines the ground-vegetation type, records it on his base map, sketching in the type boundaries as he proceeds. The mapper should be an experienced ecologist familiar with both the primary and sub-

ordinate vegetation of the region. He must also have a discerning eye for forest-type trends and succession.

From the silviculturist's point of view, the principal value of a site-type classification lies in its potentialities for identifying forest types biologically of the same value. The reaction of biologically equivalent types to long-term application of a given intensity of forest practice should be reasonably uniform. Thus an accurately developed site-type classification enables the forest manager to delineate his property into zones requiring uniform silvicultural treatment. From a forest manager's standpoint, only the extent to which the site-type classification successfully portrays biologically equivalent types justifies its application.

The site-type concept is not the one and only answer to the problem of site classification. It is not infallible. Certain radically disturbed areas may defy classification for an indeterminate period. Some foresters thoroughly familiar with the forest types of a region rely wholly on arboreal growth for site identification. Nevertheless, plant indicators used in conjunction with other site manifestations, such as tree height, tree associations, soils, and land forms, will aid in a more accurate delineation of forest sites. The dendrologist attempting to identify a tree solely by a bark sample welcomes a sample of its leaves, twigs, and flowers. So the silviculturist aiming at rational forest management welcomes any new significant factor that will enable him to identify forest site with a higher degree of accuracy.

SUMMARY

The key to sound silviculture is ecology: intelligent management of our forests cannot be achieved without thorough knowledge of the behavior of tree species and stands and their relation to their habitat. For every species or group of species there is an optimum site. To try to grow species ill adapted to the site is an open invitation to inroads by damaging diseases and insects.

Attainment of productive, resistant forests can be greatly facilitated by striving for stand compositions that are natural to the sites. The first step in a program for placing the silviculture of a region on a firm basis is the classification of its forests into climax associations natural to the site. This is not a simple undertaking in regions where repeated cutting and fire have greatly altered the composition of the original forest.

The author describes two schemes for reconstructing the original forest associations in the spruce-fir and northern hardwood regions of the Northeast (1) through interpretation of the existing forest cover types and (2) through the use of indicator plants that form part of the minor vegetation in the forest. He presents a site-type classification showing what species the forest manager should favor on sites characterized by certain ground vegetation types. Techniques of site-type mapping are described briefly.

LITERATURE CITED

- Cajander, A. K. 1926. The theory of forest types. *Acta Forest Fenn.* 29 (3): 1-108.
- Brunkman, A. H. 1936. Mosses in relation to Cajander's theory of forest types. *Forestry Chron.* 12: 300-314.
- Heiberg, S. O., and R. F. Chandler, Jr. 1941. A revised nomenclature of forest humus layers for the Northeastern United States. *Soil Sci.* 52: 87-93.
- Heimbürger, C. C. 1934. Forest type studies in the Adirondack region. Cornell Univ. Agric. Exp. Sta. Memoir 165. 122 pp.
- Hills, A. G. 1950. The use of aerial photography in mapping soil sites. *Forestry Chron.* 26: 4-37.
- Holman, H. L. 1929. Ground vegetation an index of site quality. *Forestry Chron.* 5: 7-9.
- Ilvessalo, Yrjo. 1929. Notes on some forest (site) types in North America. *Acta Forest Fenn.* 34: 1-111.
- Linteau, J. A. 1940. Vegetation et appréciation des qualités de station en forêt. *Le Forêt Québécoise* 2: 36-45.
- Losee, S. T. B. 1942. Air photographs and forest sites. *Forestry Chron.* 18: 129-144, 169-181.
- Moessner, K. E. 1948. Photo classification of forest sites. *Proc. Soc. Amer. Foresters* 1948: 278-291.

- Ray, R. G.** 1941. Site-types and rate of growth, Lake Edward (Quebec). Canada Forest Serv. Silv. Res. Note 65. 82 pp.
- Recknagel, A. B., H. L. Churchill, C. Heimbürger, and M. Westveld.** 1933. Experimental cutting of spruce and fir in the Adirondacks. Jour. Forestry 31: 680-688.
- Sisam, J. W. B.** 1938. Site as a factor in silviculture—its determination with special reference to the use of plant indicators. Canada Forest Serv. Silv. Res. Note 54. 90 pp.
- Society of American Foresters.** 1932. Forest cover types of the eastern United States. Report of the committee on forest types. Jour. Forestry 30: 451-498.

POLLEN SUCCESSION IN THE SEDIMENTS OF SINGLE-TARY LAKE, NORTH CAROLINA¹

DAVID G. FREY

Zoology Department, Indiana University, Bloomington

In an attempt to unravel the complicated ontogeny of some natural lakes in the North Carolina Coastal Plain on the basis of their accumulated sediments, the writer was led into the analysis of the plant and animal remains contained in them. Pollens and spores, primarily those of aerial plants, are by far the most abundant of all microfossils in these sediments, and because of their diversity and very long period of accumulation they afford an excellent means of determining the relative total age of the sediments and of correlating the sediments from various parts of the basin as to contemporaneity.

Pollen studies in eastern North America have been confined largely to the glaciated portion because of the abundance there of glacial basins filled with peat deposits. Similar studies south of the glacial boundary are few and scattered. The first of these by Lewis and Cocke (1929) and later by Cocke, Lewis, and Patrick (1934) describes the pollen and spores at various levels in the recent deposits of the Dismal Swamp near Lake Drummond in Virginia. Buell (1945) made some investigations on the sediments of Jerome Bay near Singletary Lake, but never published any comprehensive quantitative account of his findings. Cain (1944) reported on the pollen content of some buried soils in South Carolina, but these at present cannot be fitted into an overall chronology of the region for the determination of their relative age. Sears (1935) presented a few diagrams for Arkansas and eastern

Tennessee. Darlington (1943) recorded the pollen sequence in a bog in West Virginia. Potzger (1945) shows a few diagrams from southern New Jersey. And finally, Potzger and Tharp (1947) present a significant pollen diagram from a bog in Texas. These analyses are still too scattered and often too fragmentary for one to draw generalizations or to try to find south of the glacial boundary the several postglacial climatic periods that have been established for the glaciated region. (See Deevey 1949, for a review of this problem.) The one generalization that can be made is that all of these southern diagrams which extend back far enough show spruce, and sometimes fir, in the lowermost horizons. It has been surmised that such horizons are from the Pleistocene.

DESCRIPTION OF LAKE AND SAMPLING METHODS

Singletary Lake is one of the few remaining "bay" lakes in the Atlantic Coastal Plain (Frey 1949). It lies in an oval basin, oriented approximately northwest-southeast, with an area of 1022 acres. The present lake covers only 569 acres of the basin area, the difference representing the amount of obliteration of lake area by accumulation of sediments, primarily peat. The sand rim surrounding the basin is sparsely covered with longleaf pine (*Pinus palustris*), turkey oak (*Quercus catesbaei*), and wire grass (*Aristida* sp.) whereas the vegetation of the filled-in portion is a highly contrasting community of broadleaf trees and shrubs, mainly evergreens, with some pond pines (*Pinus serotina*), white cedars (*Chamaecyparis thyoides*), and a few cypresses (*Taxodium distichum*) in local stands. There is no surface inflow from outside the sand rim

¹ Field work in this problem was aided financially by grants C-50 and C-63 from the Carnegie Foundation for the Advancement of Teaching while the author was at the University of North Carolina. The author wishes to acknowledge the assistance of H. T. Odum and R. W. Borden in carrying out the necessary field work.

into the lake, although there is a small outlet towards the east end, which is frequently dry in summer. A concrete spillway was constructed in this outlet about 1936 to help control the level of the lake. Thus the entire watershed is not even twice as large as the present area of the lake. The lake is shallow, with the deepest portion (just under 12 feet) occurring near the southeast end.

In 1948 cores were taken at intervals of approximately 500 feet along a longitudinal transect of the lake. Samples of the softer surface materials were collected most conveniently with a Davis peat sampler. Samples from the deeper sediments, and especially the sand, were obtained with a Wilson sampler (Wilson 1941), which employs a jet of water to loosen the materials and thereby permits the pipe to be worked into them. At each station samples were collected at intervals to the greatest depth possible with the manpower available.

In 1949, as part of an expanded approach to the general problem of the Carolina bays, the transect was extended through the filled-in portion of the basin at the northwest end of the lake. A Davis sampler was used throughout in this work, and sampling was necessarily stopped when sand was reached. For further work in the lake basin itself a Hiller-type sampler was used to obtain samples from the superficial layers of sediments. A contour map was also prepared of the sand floor underlying the softer organic and inorganic sediments of the present lake. Three distinct basins were found, two underlying the present lake area and one beneath the filled-in portion at the northwest end. The present paper is a report on the pollen succession in the deepest core from each of these basins, namely Si-25 from the southeast basin (depth 21 ft. 7 in.), Si-12 from the middle basin (19 ft. 6 in.), and Si-22 from the northwest basin (17 ft. 7 in.).² All 3 cores show a surface organic layer,

which in the case of Si-22 extends to or slightly above the present water level. Beneath this is a layer of whitish silt, which overlies a second organic layer at a depth from 14 to 16 feet below the surface of the lake and extending downward for 2 to 3 feet. Below this second organic layer is sand, except in the case of Si-25, where sandy silt occurs, overlying a third somewhat indefinite organic layer, which in turn rests on sand.

LABORATORY PROCEDURES

Slides from sediments consisting almost entirely of organic material were prepared according to a standard technique of boiling a small amount of the material in 10% KOH. After washing and concentrating by centrifugation, a portion of the material was mounted in glycerine jelly containing gentian violet.

Samples from the silt layers contained so few pollen grains that some concentration technique was necessary. After considerable experimentation a modification of the procedure recommended by Knox (1942) was adopted. This is believed superior to the HF technique in the present study, because it permits recovery of sponge spicules, diatom frustules, and other silicious remains, as well as of pollen and spores. It is given in some detail for those who may have similar sediments to study.

1. Make up a mixture of bromoform and acetone adjusted to a specific gravity of 2.3.

2. Place a portion of the sediment about the size of a pea in a beaker with perhaps 20 cc. of 10% KOH and boil until all clumps have disintegrated and the material is of uniform consistency. If there is sand in the sample, the beaker may have to be constantly rotated to prevent bumping.

3. Centrifuge, decant, resuspend in water, and centrifuge again. Decant. (A camel's hair brush was the best means found for resuspending the material in these various operations.)

² All depths are referred to the crest of the spillway at the outlet of the lake.

4. Suspend in acetone and centrifuge. Decant.

5. Suspend in 5 cc. bromoform mixture and centrifuge. The organic material plus many of the spicules and other siliceous remains come to the top. Decant. (Step 5 was usually repeated on the material at the bottom of the tube.)

6. Dilute the supernatant liquid with its pollen, etc., with at least an equal volume of acetone and centrifuge. Decant.

7. Suspend in acetone and centrifuge. Decant.

8. Suspend in a small amount of 95% alcohol and mount directly in glycerine jelly containing gentian violet.

With continuous attention one can prepare slides by this method at the rate of 3 or 4 per hour.

Sand samples involved some variation of the procedure described above. A teaspoonful of sand was boiled in 10% KOH in a beaker continually moved with a twirling action to prevent bumping. The liquid was set in vigorous motion to suspend all small particles and then decanted. This was repeated a second time and even a third time if it seemed necessary. The decanted material was then run through the procedure described above to get rid of most of the silt and clay.

In making the necessary quantitative counts, the slides were examined systematically with a mechanical stage at a magnification of 440 $\times$, and all pollens and spores were tabulated as encountered. The examination was not terminated until at least 150 tree pollens had been found. In the pollen diagrams to follow all types of pollen and spores are expressed as percentages of the total arboreal pollens observed.

RESULTS AND DISCUSSION

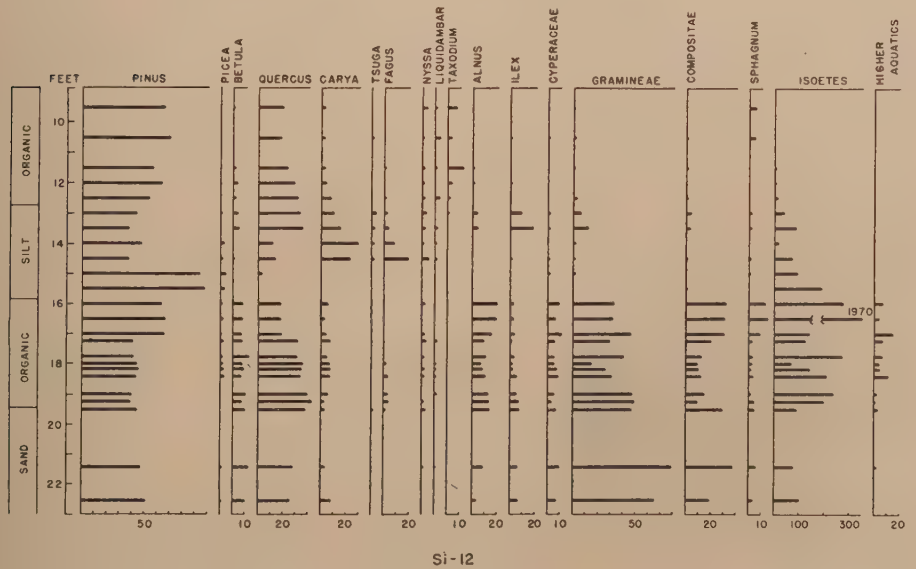
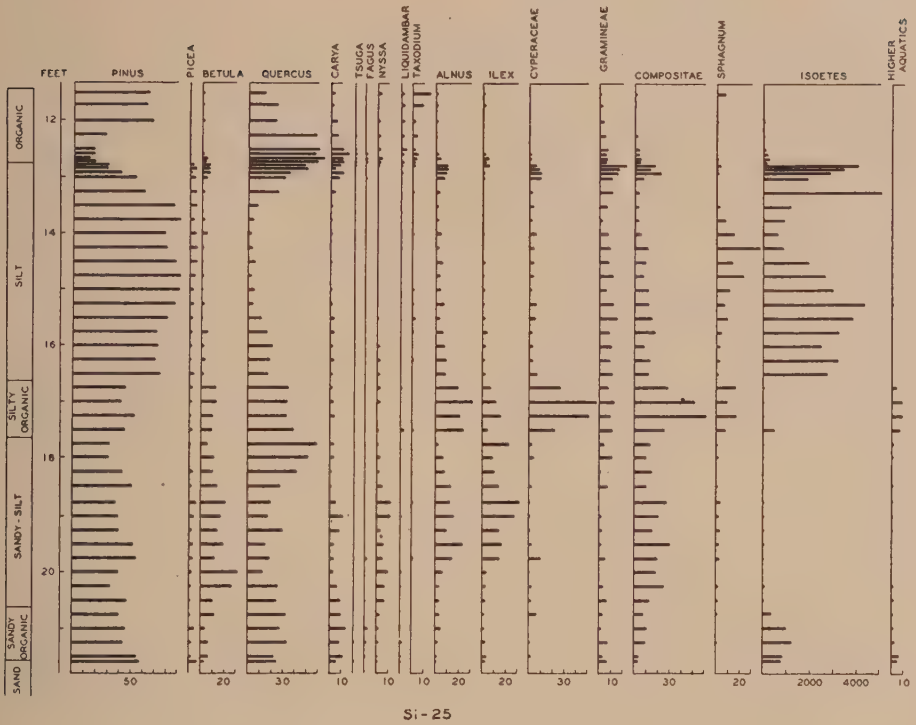
So many different kinds of pollen and spores were found at one time or another that it would not be practicable to show all of them in a pollen diagram. Instead, only the major tree species are shown, plus those shrubs and herbaceous types that appear to be most important in terms

of their total occurrence, their usefulness in interpreting conditions inside and outside the lake itself, and their value in helping to make stratigraphic correlations from one part of the lake to another. The following list of the generic and common names of the trees mentioned in this study is given to prevent ambiguity:

Abies—fir
Acer—maple
Betula—birch
Carpinus—bluebeech
Carya—hickory
Castanea—chestnut
Chamaecyparis—swamp whitecedar
Fagus—beech
Fraxinus—ash
Juglans—walnut
Liquidambar—sweetgum
Nyssa—tupelo
Ostrya—hophornbeam
Quercus—oak
Picea—spruce
Pinus—pine
Salix—willow
Taxodium—cypress
Tilia—basswood
Tsuga—hemlock
Ulmus—elm

Figures 1, 2, and 3 are the pollen diagrams from the three described locations in the lake. Although there are some rather marked differences in proportion of the various pollens and spores from one core to another, still the major features are the same in all. On the basis of past experience a considerable amount of variation is to be expected in pollen analyses even from adjacent locations, but in the present study the variation is undoubtedly heightened by the very slow rate of sedimentation, resulting in pronounced vegetational changes being compressed into short vertical distances.

There is no spruce in the North Carolina Coastal Plain at present, but in all three diagrams spruce pollen appears at a particular level and then continues almost without interruption to the bottom of the cores. A short distance below



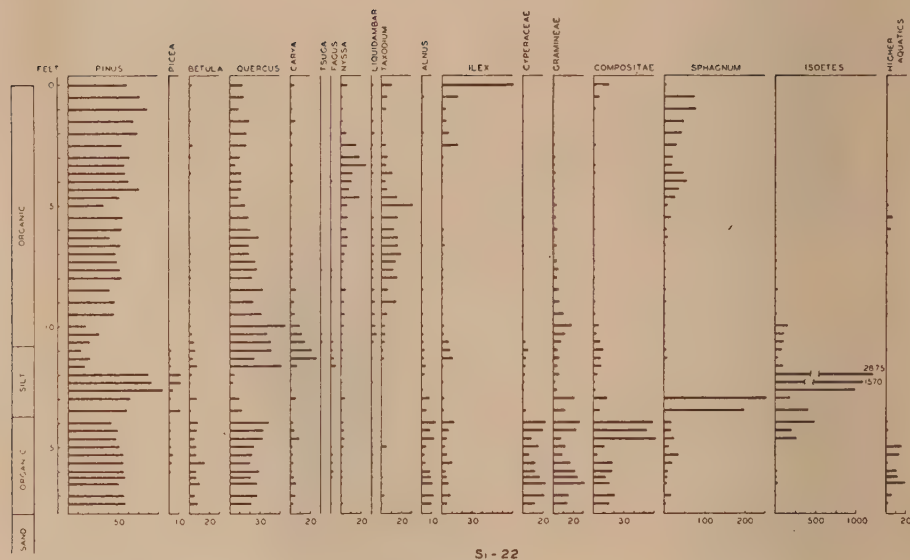


FIG. 3. Pollen diagram of core Si-22 from the northwest basin of Singletary Lake.

where the spruce first appears there is at a depth of 12 to 15 feet a marked pine-spruce maximum, with almost no broad-leaf trees represented. This zone is considered to be contemporaneous with the last glacial maximum (Mankato), and with respect to the vegetation shown in these sections it represents the most severe climatic conditions encountered. This does not mean that North Carolina was being affected directly by the glaciation several hundred miles to the north and northwest, but rather that it and other parts of the South were sharing in the general depression in climate that was responsible for the ice sheets. The simultaneous occurrence of glaciers in widely scattered loci in the Northern Hemisphere in Pleistocene time adequately demonstrates this point.

Complete pollen diagrams from the glaciated region begin with a spruce-fir maximum, which would be somewhat younger in an absolute time scale than the pine-spruce maximum in these diagrams. Hence, everything below this level represents a considerable extension of our knowledge concerning Pleistocene

climatic and vegetation changes in eastern North America, with the exception of the late-glacial pollen diagrams from Maine recently presented by Deevey (1951).

Post-Mankato-maximum pollen succession

Above the pine-spruce maximum there is a sudden and dramatic shift to a beech-hickory-oak dominance, with some hemlock and birch mixed in. According to cores Si-22 and Si-12, which have the thickest postglacial records, it appears that in this general level the beech maximum occurs earliest, followed in rapid succession by maxima of hickory and then oak. The earlier portion of this broadleaf succession containing the mesophytic beech and hemlock corresponds to the C1 zone of the northern United States, and the upper portion containing a small grass maximum along with the oaks corresponds to the warm, dry C2 zone (Deevey 1949).

Above the oak maximum (shown best in core Si-25) there is a pronounced maximum of cypress pollen, then a maximum of tupelo, followed by a second increase

in cypress. These two latter increases are associated with increases in *Sphagnum*, and all of them together seem to indicate a definitely moister climate than formerly, corresponding to Deevey's C3 zone. In addition the marked increase in pine pollen above the oak maximum probably indicates a cooling climate. Hence, much of the filling in of the north-west end of Singletary Lake has occurred since the thermal maximum (C2). The rate of sedimentation has apparently been greater since the oak maximum than immediately before.

Below the C1 zone in northern profiles there is a B zone, represented by a pine maximum, and a still older A zone, distinguished by a spruce-fir maximum. Both of these zones are missing in the present diagrams. The shift in climate appears to have been directly from cool (pine-spruce) to warm, moist (beech-hemlock-hickory), without any intermediate dry stage. Apparently the A and B zones of the northern profiles represent concentric periglacial conditions that did not occur so far south of the glacial boundary as southeastern North Carolina. The pine-spruce maximum of the present pollen diagrams would antedate any A zone from the glaciated region.

Recently age determinations by the radiocarbon method have been reported for various horizons, chiefly from Mankato-maximum and post-Mankato-maximum time (Arnold and Libby 1951). Flint and Deevey (1951) concluded on the basis of these analyses that the Mankato maximum at Two Creeks, Wisconsin, was approximately 11,000 years ago. The B zone in pollen stratigraphy exhibits an increasing age towards the south, from approximately 6,000 years in Plissey Pond, Maine (Sample No. 335), to 9,400 years in Cranberry Glades, West Virginia (No. 336), the latter location being peripheral to the glacial boundary. This is the type of latitudinal time sequence one would expect in a periglacial vegetation.

The contact between the light gray silt

and the dark organic silt at site Si-25 is very sharp, suggesting an unconformity although there is no evidence of any discontinuity in the pollen record. A composite sample representing 30 shots with a Hiller sampler of the three inches of sediment immediately overlying this plane of contact was submitted for radiocarbon analysis. The calculated age of this sample is $10,224 \pm 510$ years (Sample No. 474, as quoted by Flint and Deevey 1951). Reference to Figure 1 shows that the zone represented includes most of the hemlock-beech-hickory-oak maximum, hence most of the C1 zone plus the lowermost portion of the C2 zone.

Flint and Deevey expressed the hope that the Mankato maximum was reached simultaneously 11,000 years ago along all or much of the glacial front. Assuming that the pine-spruce maximum in Singletary Lake does in fact represent the Mankato maximum, as seems likely from its position inferior to the C1-C2 stratum with a known age of approximately 10,000 years, then on purely circumstantial grounds it does not seem reasonable that the pine-spruce maximum is only 11,000 years old. At site Si-25 just 14 inches of sediments have accumulated in the past 10,000 years, whereas if the pine-spruce maximum is only 11,000 years old, then 23 inches of sediments accumulated in the 800 years prior to the radiocarbon date cited. Quite likely the rate of sedimentation was considerably greater during the glacial sub-ages as a result of wind-blown material, but the author is hesitant to believe that it was 20 or more times greater.

The time of the thermal maximum is not yet satisfactorily fixed by the radiocarbon method. Sub-Boreal time in Europe is generally believed to have extended from 7,500 to 2,500 years ago. The C2 climatic phase in North America seems to have begun somewhat more than 5,000 years ago. The inconclusive dates suggest that the age of the C1 zone at Singletary Lake is greater than ex-

pected, especially when it is remembered that the sample analyzed contained a certain proportion of the overlying C2 material, which would tend to reduce the radiocarbon age of the composite sample below that of the C1 zone alone. If the above reasoning is correct, then the beginning of the first broadleaf climatic phase (C1) was determined at least in part by conditions accompanying deglaciation. If the thermal maximum (C2) was determined by conditions primarily of extraterrestrial origin, as currently believed, then the duration of the preceding C1 zone should become greater towards the south.

*Pre-Mankato-maximum pollen
succession*

Below the pine-spruce maximum spruce pollen is continuously present except for a thin stratum in the lower portion of the middle organic layer. From the pine-spruce maximum to the bottom of the second organic layer there is a fairly gradual decline in pine and a corresponding increase in oak to a distinct maximum in core Si-25. Birch likewise increases to a respectable percentage, and there are fairly consistent, although not large, percentages of *Carya*. Both hemlock and beech recur somewhere near the oak maximum, and chestnut (not shown in the diagrams) is more abundant just above the oak maximum than at any other place in the cores. These various mesophytic types indicate that the climate was fairly moist as well as warm at this time.

Most-characteristic of this second organic layer, however, are the large percentages of *Alnus*, *Ilex*; sedges (Cyperaceae), grasses (Gramineae), composites, and the pollen of higher aquatics (*Myriophyllum*, *Nymphaea*, *Nuphar*, *Utricularia*, *Eriocaulon*) occurring at this time. These features are uniform in all three diagrams. An abundance of grasses, composites, and sedges is usually taken to indicate an open type of vegetation with only scattered trees, rather than

mainly woodland. This is particularly true where the percentages of these types exceed the total tree pollens, as they do in a number of instances in the samples from the second organic layer.

The most abundant microfossils in the three cores were the microspores of *Isoetes*. There appear to be two maxima, one at the general level of the pine-spruce maximum and the other a short distance below. The microspores are present in relatively small numbers in the second organic layer, and they disappear rapidly and completely after the thermal maximum. Radford (1950) has recently found *Isoetes* quite widespread in the Coastal Plain of North Carolina, where it occurs in slowly moving streams and on black muddy stream banks. It is less commonly encountered in the brown, acid waters of this region. The maximum abundance of *Isoetes* microspores was 5,050 per cent at 13.25 ft. in core Si-25. This far surpasses the previously reported maximum of 300.5 per cent in European deposits (Oberdorfer 1931).

Judging from the more complete record of these older deposits in core Si-25, the pollen records in cores Si-12 and Si-22 stop just short of the middle oak maximum, which is immediately below the second organic layer and also below the sedge-grass-composite maximum. Below this level, as shown in core Si-25, there are somewhat intricate fluctuations in pine, birch, oak, *Carya*, and *Nyssa*. In general, the oaks decline to rather low levels, then increase again somewhat in the lowest organic layer. Associated with the latter increase is a maximum of *Carya* as well as the recurrence of small percentages of hemlock and beech, indicating general mesic conditions. There are also increases in *Isoetes* and the higher aquatic plants in the same period. In the complicated interval between the middle and lowest oak maxima there are various increases in pine, birch, *Carya*, *Nyssa*, *Alnus*, and *Ilex*, the significance of which in the overall climatic changes is not yet known. It may be

significant from a successional aspect that each of the two *Carya maxima* in this general period is followed by a *Nyssa-Betula* maximum, indicating two minor periods of increasing wetness. The overall picture is that the middle and bottom organic layers each represents a milder climate than in the predominantly inorganic layers above and below. Because of the importance of core Si-25, the results are presented completely in tabular form.

There are two likely explanations of the middle and lowest organic layers: a) they are formed during periods of milder climate coincident with known glacial recessions within Wisconsin time, or b) they were formed during the much more extensive interglacial ages. If the Wisconsin recessions resulted in or were coincident with marked climatic changes south of the glacial boundary, one would certainly expect significant vegetational changes to be apparent in the pollen record.

The radiocarbon ages of five samples from the Two Creeks Forest Bed, of upper Cary-Mankato age, averaged $11,404 \pm 350$ years. Sample No. 508 from the Tazewell-Cary interval was older than 17,000 years, and sample No. 575 from the Tazewell sub-age was likewise older than 17,000 years. Other dates for pre-Mankato materials gave minimum ages ranging from 16,000 to 20,000 years. Nothing can be stated as to the actual ages of these various samples until the sensitivity of the method is increased.

A multiple-shot sample (No. 475) from a 4-inch stratum in the upper half of the middle organic layer at Si-25 gave a radiocarbon age greater than 20,000 years, and another multiple-shot sample (No. 476) from near the bottom of the third and lowest organic layer likewise yielded an age greater than 20,000 years.

If the two lower organic horizons date from interglacial sub-ages in Wisconsin time, one would expect the middle organic layer to be Cary-Mankato and the lowest layer Tazewell-Cary. On the

basis of the pre-Mankato radiocarbon dates at hand Flint and Deevey (1951) believe the middle organic layer is too old for Cary-Mankato. This interpretation would mean that the Cary-Mankato recession did not sufficiently modify the climate in North Carolina to permit the establishment of deciduous trees. As will be pointed out later, however, within the upper silt layer there are changes in the pine flora that might have been responses to climatic fluctuations.

The situation with respect to the two lower organic layers is by no means clear. It is unlikely that the middle layer is Sangamon, because of its limited extent and the almost continuous occurrence of spruce pollen. Deevey (1951) recently reported some pollen diagrams from northern Maine, the lowermost portion of which appears to be late-glacial in age. The middle L2 zone of these deposits was tentatively assigned to the Two Creeks interval. Because the non-tree pollens, particularly grasses and composites, were more abundant than the total tree pollens, Deevey concluded, according to accepted practice, that a tundra was present at this time, changing to taiga at a higher level where non-tree pollens aggregated less than 100 per cent but were still abundant.

The interesting fact is that the middle organic layer at Singletary Lake in spite of its great age exhibits many of the features found in these Maine deposits. The non-tree pollens (Ericacean pollens not shown in the diagrams amounted to slightly more than 10 per cent) frequently totalled more than 100 per cent. An increase in birch, as reported by Deevey, is also present. This does not mean that tundra conditions extended so far south as North Carolina, but certainly the country was mainly in shrubs and herbaceous types, with only a scattering of trees. There is a possibility, therefore, that the Cary sub-age lasted longer than supposed, and until the Cary maximum is more precisely dated the possibility cannot be eliminated that this layer is Cary-

TABLE I. Complete pollen and spore analysis of core Si-25.

Depth	<i>Pinus</i>	<i>Picea</i>	<i>Quercus</i>	<i>Carya</i>	<i>Betula</i>	<i>Fagus</i>	<i>Tsuga</i>	<i>Casanea</i>	<i>Nyssa</i>	<i>Liquidambar</i>	<i>Taxodium</i>	<i>Acer</i>	<i>Ulmus</i>	<i>Tilia</i>	<i>Fraxinus</i>	<i>Juglans</i>	<i>Salix</i>	<i>Carpinus</i>	Total tree pollens	<i>Alnus</i>	<i>Ilex</i>	Ericads
11'6"	64.5		12.5	2.1	1.0		+	1.0	2.1	1.6	14.1	0.5	0.5						192	0.5	0.5	0.5
11'9"	62.7		23.9	1.4	0.5			0.5		1.9	8.1		0.5						209	0.5	1.0	0.5
12'0"	67.4		22.7	4.7	1.2				0.6	2.3	1.2								172	0.6		1.2
12'3"	27.9		57.0	5.6				0.6	1.1	1.7	3.4		1.7					0.6	179			
12'6"	18.2		59.7	10.2			0.6	1.1	1.1	4.0	1.1		3.4		0.6				176			0.6
12'7"	17.7		56.9	14.6	1.1		0.6	1.7	1.1	3.9			0.6						178	1.7	1.7	1.1
12'8"	13.4		63.5	9.5	3.6		0.6	1.2	0.6	2.4			0.6		1.2			1.2	169	3.0	4.2	0.6
12'9" above	18.8		58.8	11.2	2.2		0.6	1.1	1.7	1.7			1.7			0.6			179		1.7	
12'9" below	30.2	2.1	47.3	8.4	6.6		0.6		0.6	0.6	1.2		0.6		1.2		0.6		167	10.2	4.2	1.8
12'10"	28.7	4.4	50.0	3.8	6.3			1.3					0.6		1.9		1.3		160	10.0		1.3
12'11"	40.8	1.2	34.8	10.4	6.4			0.6		0.6			1.7		1.2		1.2	0.6	173	8.1	0.6	0.6
13'0"	53.9	3.8	30.3	6.9	3.8		0.6								0.6				159	6.3	0.6	0.6
13'3"	60.9	5.1	25.6	3.8	1.3						0.6				1.3			1.3	156	2.6		0.6
13'6"	86.4	4.7	7.7	0.6													0.6		169	1.2		0.6
13'9"	91.6	3.0	2.7	0.7	2.0														151	2.0		1.3
14'0"	88.4	4.6	1.7	0.6	4.1						0.6								173	3.5	0.6	3.5
14'3"	89.8	5.8	3.1		0.6												0.6		163	1.2		4.5
14'6"	87.8	5.8	5.1	0.6	0.6														156	5.1	1.9	4.5
14'9"	91.5	4.2	2.4		1.2														165	3.0	0.6	2.4
15'0"	90.8	2.2	4.4	0.6	0.6						0.6		0.6				0.6		159	3.8	1.3	1.3
15'3"	87.6	3.1	3.7	0.6	2.5						0.6			0.6				0.6	162	6.8	1.2	5.6
15'6"	80.3	1.6	11.0	2.6	0.6			1.9	0.6		1.3								155	2.6	1.3	3.2
15'9"	72.0	1.9	16.9	2.6	5.2			0.6			0.6				0.6				154	5.8	3.9	2.6
16'0"	72.7	1.3	20.9	1.3	1.3				1.3	1.9			0.6					0.6	158	7.0	1.9	0.6
16'3"	70.9	1.0	18.5	2.6	2.6			1.3	1.9					0.6					157	8.9	1.3	5.1
16'6"	75.0	3.7	16.2	1.3	1.3			0.6	1.9										160	8.1	1.9	1.9
16'9"	45.4	2.0	34.2	1.3	12.5			1.3	2.6	0.7									152	19.1	7.2	10.5
17'0"	42.2	1.3	33.3	2.5	13.2			1.3	2.5			0.6	0.6					1.3	159	31.5	11.9	10.7
17'3"	53.0	0.3	32.6	3.8	9.6									0.6					157	21.1	15.3	7.0
17'6"	44.8	1.6	38.7	2.6	9.0			0.6	0.6	0.6	0.6						0.6		155	23.9	4.5	3.9
17'9"	31.9	0.3	58.2	3.4	5.6				0.6										179	2.8	23.0	
18'0"	31.2	+	50.9	2.3	11.0				2.3			0.6	0.6						173	6.4	8.7	
18'3"	42.2	2.4	41.6	0.6	10.2				1.8									0.6	166	7.8	9.6	1.8
18'6"	50.8	1.2	27.7	0.6	13.5				4.9									1.2	163	13.5	14.2	
18'9"	36.7	5.1	19.2	4.5	20.4			1.3	11.5		0.6								157	12.1	31.3	1.9
19'0"	38.7	3.5	17.1	10.8	17.1				11.4	0.6									158	15.9	27.3	1.9
19'3"	39.0	1.8	29.9	8.5	14.0			0.6	3.7										164	9.7	14.6	2.4
19'6"	51.8	2.6	14.9	3.9	19.3				5.8										156	23.1	16.7	1.9
19'9"	54.1	3.1	18.6	3.1	11.2	1.2		0.6	4.3		0.6	0.6		0.6				1.2	161	14.3	14.9	0.6
20'0"	39.3	2.1	13.3	3.0	32.0				9.7	0.6									166	6.6	3.6	1.2
20'3"	32.5	1.3	25.2	6.6	26.5				6.6	0.7								0.7	151	3.3	2.6	0.7
20'6"	46.3	1.2	24.4	8.5	10.4	0.6			6.7			0.6						1.2	164	3.0	2.4	
20'9"	39.9	1.2	32.2	9.9	11.1			0.6	2.5				0.6		1.2			0.6	162	3.7	1.9	1.2
21'0"	45.2	4.3	27.5	13.8	3.9	2.0		0.7	1.3									1.3	153	4.6	1.3	3.3
21'3"	43.9	1.9	33.5	8.4	5.8	1.3			1.3	1.3			0.6	0.6				0.6	155	2.6	3.2	1.9
21'6"	54.5	1.8	22.4	11.5	6.7	0.6			0.6	0.6					0.6				165	1.8	4.2	
21'7"	57.0	7.3	24.5	5.3	3.3		0.7		1.3	0.7									151	1.3	3.3	1.3

Mankato rather than Tazewell-Cary or some greater age.

Assuming the age of the pine-spruce maximum at 11,000 years and assuming a constant rate of sedimentation, the age of the lowermost sediments at Si-25 would be 37,000 years. On the other hand, on the basis of the rate of sedimentation since the radiocarbon age of 10,224 years in the C1 zone, the age of

the lowermost sediments would be 99,000 years. Whatever the basis for estimation, Singletary basin certainly extends far back into Wisconsin time and may conceivably break through into the Sangamon.

It is remarkable that a lake of such shallow depth could have been in existence for such a long period of time. The accumulation of organic sediments

All figures are percentages of the total tree pollens at each level

<i>Corylus</i>	<i>Myrica</i>	<i>Viburnum</i>	Gramineae	Compositae	Cyperaceae	Chenopods	Caryophyllaceae	<i>Nuphar</i>	<i>Nymphaea</i>	<i>Myriophyllum</i>	<i>Utricularia</i>	<i>Ericaulon</i>	<i>Isoetes</i> microspores	<i>Isoetes</i> megaspores	Lycopods	Polypods	<i>Asplenium</i>	<i>Sphagnum</i>	"Cysts"	Unidentified	Depth
0.6	0.5		0.5 1.0 2.9 3.9	0.5 1.7 3.4 5.1 6.5 5.0		0.6 0.6							2.9 12.3 47.7 134 215 125		1.6 0.6 0.6 1.8 0.6	2.1 1.2		6.8 0.6 0.6	0.5 4.1 8.9 5.7 10.1 5.3 3.4	26.0 13.4 25.6 34.1 42.8 61.1 35.8	11'6" 11'9" 12'0" 12'3" 12'6" 12'7" 12'8" 12'9" above
0.6		0.7	22.7 16.3 15.1 10.1 10.3 5.9 1.3 7.0 8.6 8.3 10.9 5.7 11.1 15.5 7.8 10.1 8.9 10.6	16.8 13.1 22.0 7.6 3.2 3.0 2.7 4.6 11.1 9.0 7.3 12.0 11.7 14.8 16.9 8.2 13.4 11.9	5.4 7.5 9.3 9.5 1.3 3.0 0.7 0.6 3.7 3.2 3.0 1.9 4.9 4.5 1.9 2.5 2.6 5.6		1.3 1.2 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6					0.6	4050 3460 2850 1875 5050 1310 866 602 864 1940 2640 2980 4300 3820 3260 2490 3210 2750		1.8 0.6 5.8 0.6 1.3 2.6 0.7 1.2 8.6 3.8 5.5 1.9 1.2 1.3 3.2 2.5 2.6 1.3	1.2 1.3 3.2 4.2 0.6 0.6 1.3 1.7 2.5 3.2 3.8 2.3 1.9 1.3 1.9 1.9 1.2 1.3 3.2 2.6 1.9	1.8 0.6 0.6 1.2 0.6 0.6 0.7 8.7 6.8 13.5 23.0 11.4 6.8 8.4 3.9 3.2 0.6 1.3	3.6 0.6 53.6 51.9 13.0 6.6 15.1 36.9 12.3 16.7 10.9 10.7 16.7 16.1 18.8 25.3 21.7 20.0	26.3 36.9 52.2 53.6 21.9 2.0 5.2 49.2 51.3 46.7 41.7 48.2 42.6 45.5 58.2 47.3 45.0	80.8 70.6 63.2 41.7 35.2 10.0 22.6 49.2 51.3 46.7 41.7 48.2 42.6 45.5 58.2 47.3 45.0	12'9" below 12'10" 12'11" 13'0" 13'3" 13'6" 13'9" 14'0" 14'3" 14'6" 14'9" 15'0" 15'3" 15'6" 15'9" 16'0" 16'3" 16'6"
0.7 1.9 1.3		3.9	7.9 12.6 8.9 11.0	28.9 51.6 61.3 25.6	27.6 57.9 51.1 21.9		0.6	2.0 2.5 3.2 2.6	2.0 2.5 1.9	0.6 0.6			17.8 3.8 4.5 479		3.9 3.1 7.7 3.9	0.6 0.6 1.3	16.4 9.4 16.6 7.7		131 236 185 155	16'9" 17'0" 17'3" 17'6"	
1.1 0.6 1.8 1.8 3.2 0.6 0.6 1.2 0.6			3.4 11.0 1.2 6.6 1.9 2.4 1.3 5.6 3.3 6.7	14.0 10.4 14.5 11.1 20.3 15.9 30.2 19.9 25.2 12.8	2.2 3.5 1.8 0.6 0.6 1.2 2.6 9.9 2.6 1.8	0.6	0.6 0.6		0.6 0.6 0.6 0.6 0.6 0.6 0.6 0.6 1.3 0.6		0.6	1.1 1.2 0.6 1.2 9.6 0.6 3.0 12.2 5.6 2.4 42.4 63.4		1.1 2.2 2.3 4.3 2.6 4.4 4.3 2.6 1.2 1.2 0.6 0.6	2.2 3.0 1.2 0.6 11.5 9.5 4.3 9.6 6.2 6.2 1.2 1.2	0.6 1.7 0.6 0.6 3.8 1.9 3.0 2.6 1.2 1.2 1.3 1.8		170 195 200 367 239 294 309 406 256 146 158 133	17'9" 18'0" 18'3" 18'6" 18'9" 19'0" 19'3" 19'6" 19'9" 20'0" 20'3" 20'6"		
0.6 0.7 1.2			3.1 2.0 7.1 3.0 6.6	7.4 10.5 9.7 4.2 4.0	6.8 0.6 1.2	0.6		0.6 0.6 1.8 0.7	1.3 1.3 1.8 2.6	0.6 0.6			328 992 1240 878 780		0.6 0.6 1.2 0.7	0.7	0.6 0.6	1.2 1.3 1.3 1.2 3.3	130 74.7 65.8 67.8 90.0	20'9" 21'0" 21'3" 21'6" 21'7"	

can occur rapidly, as witnessed by the acceleration in rate of sedimentation at the northwest end of the basin since the thermal maximum. The silt that is so abundant in Singletary Lake and in nearly all other bays investigated to date (Frey 1950) is probably wind transported material or loess from the outwash plains exposed during glacial ages and sub-ages. The pre-Mankato portion

of the record in the sediments is complicated by the fact that some of the deposits may have been reworked by waves and currents. Any discontinuities in the record from complete desiccation and subsequent erosion could have been obscured by a later reworking of the sediments at the unconformities. Certainly the sediments laid down in post-Mankato time are largely in place, and it is further

believed that most of the material deposited during pre-Mankato time is substantially intact. Only additional long records from other localities will aid in deciding this matter.

Species composition

The two most abundant types of trees in these diagrams—oaks and pines—are each represented by such a variety of species in the North Carolina region that identification of species on the basis of pollen grains is virtually impossible. Cain (1940) studying the size-frequency distributions of pollens of the various species of pines found such a great overlapping of arrays that identification of individual grains was not possible, although if not more than 2 or 3 species were present in a particular sample they might be identified by fitting known frequency curves to the modes of the overall size-frequency distribution. Using this technique he concluded for some buried soils in South Carolina, and Buell (1945) likewise concluded for the lowermost sediments in Jerome Bay near Singletary Lake, that one of the dominant pines present in association with spruce was *P. Banksiana*, a species now completely absent from the South. Both Buell, and Cain and Cain (1948a) were disturbed by the fact that the size of fossil pollen averaged less than that of fresh pollen from supposedly the same species. This was accounted for by a loss in ability of the grains to swell when placed in aqueous or glycerine media. Another explanation is suggested by the findings of Cain and Cain (1948b) that the pollen of present day *P. echinata* from the southern part of its range tends to be smaller than that from the northern part. These difficulties all combine to make the recognition of fossil pollen by the statistics of extant populations hazardous.

In spite of this it is instructive to examine the distribution of grain size at various levels in core Si-25 (Fig. 4). At each level shown the internal diameter (not including the marginal crest)

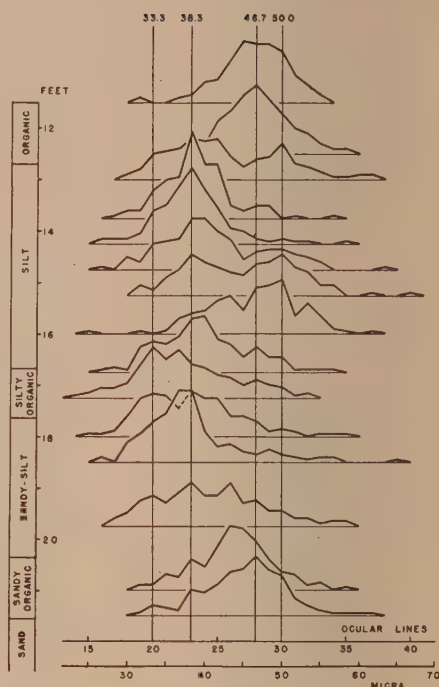


FIG. 4. Fluctuations in size-frequency distribution of pine pollen from various levels in core Si-25. Each curve is based on the measurement of the interior body length of 150 pollen grains.

of 150 grains was measured to the nearest 1.67μ with an ocular micrometer. The actual location of the modes of these frequency curves is probably not significant, inasmuch as all the species studied by Cain (1940) had mean lengths (including marginal crests) in excess of 50μ , except for *P. Banksiana*, the pine with the smallest grains. The relative positions of the maxima, however, show that there have undoubtedly been extensive shifts in composition and in the proportion of the species present during the period of time represented by this core.

At the time of the pine-spruce maximum at 13.75 ft. there is a prominent mode at 38.3μ and a lesser one at 46.7μ . This distribution changes rapidly to a unimodal curve at 12.5 ft. with a maximum frequency at 46.7μ , which persists up to the

surface sediments. This latter curve probably is made up largely of *P. serotina*, *P. palustris*, *P. taeda*, and *P. echinata*, which are the most abundant pines of the region at present. The mean size of fresh grains of these species according to Cain (1940) varies from 62 to 69 μ , indicating a "shrinkage" in the fossil and sub-fossil grains of approximately 29 per cent. If the mode at 38.3 μ is that of *P. Banksiana*, as Cain and Buell have suggested for similar horizons, then the shrinkage of this species amounted to only 13 per cent from the present mean size of approximately 44 μ established by Cain and Cain (1948a) and Buell (1946). Either the amount of shrinkage can vary from species to species, or the species forming the mode at 38.3 μ is not *P. Banksiana*. In partial support of the latter point of view is the mode at lower levels at the even smaller grain size of 33.3 μ . Assuming that this latter mode is *P. Banksiana*, however, does not dovetail with the facts in the pollen diagram, because this mode is best represented in and just below the middle organic layer where climatic conditions, as indicated by the overall pollen spectrum, appear to have been generally different from those occurring in the present range of the species. Until other more certain means of identification are worked out, it is perhaps advisable to leave all these pines as "unidentified."

Climatic conditions throughout the upper silt layer were apparently not nearly so uniform as might be deduced from the pollen diagrams alone. Large grained species of pines are much more abundant near the lower part of this layer than in the upper half or at the bottom, indicating a marked change in pine flora during deposition of this silt without any corresponding change in the other tree species. The only apparent concurrent changes are a maximum of *Isoetes*, and minor peaks of composites, grasses, sedges, and *Alnus*. If the middle organic layer eventually is found to date from the Tazewell-Cary interval, then this zone of increased mean

size of pine pollen from 15 ft. 3 in. to 16 ft. may well represent the response to the glacial recession during the Cary-Mankato interval. A frequency distribution more or less similar to that in the surface sediments is not re-encountered until the very bottom of the core. With such marked fluctuations in species composition it is unfortunate that the actual species cannot be determined. Camera lucida sketches of a small and a large pine grain are given in Figure 5, A and B.

With respect to spruce, Cain (1948) has shown that there are marked differences in size of the 3 species in eastern North America, as well as rather pronounced differences in shape of the pollen grains. It is believed that 2 species occur in the present material. The most frequent type is a large grain with small bladders, shown in Figure 5, C. This is believed to be *Picea glauca*. A less abundant and smaller grain, scarcely larger than the largest pine grains encountered, with more prominent bladders than in *P. glauca*, compares well in size and shape with the description of *P. mariana*. Such a grain is shown in Figure 5, D.

Fir was present in such low abundance that not a single grain was encountered during the regular pollen counts. Several grains were observed, however, and one of them, typical in shape although well below the average size, is shown in Figure 5, F.

Hemlock is another type that does not now occur in the North Carolina Coastal Plain, although it occurs in the mountains and in the upper Piedmont. Small percentages of this conifer were encountered at levels already indicated. A typical hemlock grain is shown in Figure 5, E, with the surface detail partly filled in.

Lewis and Cocke (1929) reported that the thin-walled grains of *Taxodium* and *Chamaecyparis* are fragile and not readily preserved. Yet in the present study, particularly in the sediments deposited since the pine-spruce maximum, substantial percentages of grains were found that can be referred with certainty to *Taxodium* or

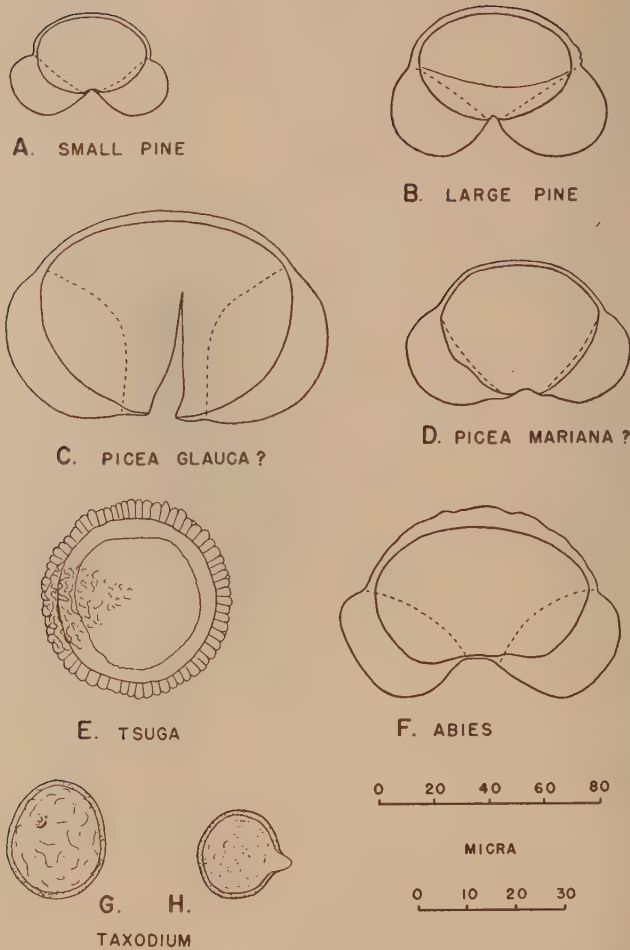


FIG. 5. Camera lucida sketches of various types of fossil coniferous pollens: A—small pine, Si-22, 12.0 ft.; B—large pine, Si-25, 16.0 ft.; C—*Picea glauca*?, Si-22, 12.0 ft.; D—*Picea mariana*?, Si-25, 16.0 ft.; E—*Tsuga*, Si-25, 12.5 ft.; F—*Abies*, Si-25, 21.0 ft.; G—*Taxodium*, surface view, Si-22, 5.0 ft.; H—*Taxodium*, side view showing papilla, Si-22, 5.0 ft.

with less certainty to *Chamaecyparis*. Pollen grains of both these types are thin-walled and superficially resemble grasses. The wall, however, is less uniform and sharp in appearance, and frequently is papillose or faintly rugose. The grains of *Taxodium* have a more or less well developed conical papilla (Fig. 5, G and H), which when seen from the side is distinct enough but when seen from the front

somewhat resembles the pore of a grass pollen. *Chamaecyparis* does not have such a papilla. Because of the difficulty in separating these two genera, any grains which might have been those of *Chamaecyparis* are included in the *Taxodium* totals. By far the greater percentage of the grains encountered were thought to be *Taxodium*.

At many levels the microspores of

Isoetes were the most abundant of all recognizable remains, being frequently 10 to 50 times as abundant as all tree pollens. Megaspores by comparison occurred only in small numbers. Two species of *Isoetes* are known from North Carolina at present, *I. Engelmanni* and its variety *caroliniana*, and *I. saccharata* (Radford 1950). Camera lucida outlines of the fossil microspores as seen from different angles are shown in Figure 6, I, J, and K, and similar views of fresh microspores of *I. Engelmanni* are shown for comparison (L, M, N, and O). The size of the fossil microspores based on 100 measurements is $22.3 \pm 0.19 \mu$, with a range of 17 to 27μ . The

surface is nearly always smooth, and only faintly papillose in a small minority of the spores. The size of 63 megaspores varied from 213 to 412μ , with a mean size of 316μ . Usually the entire surface of the megaspores was apparently smooth, as in Figure 6, Q, although in a considerable number there were short, irregular, non-anastomosing rugae on the apical surface, as in Figure 6, P. Perhaps the most characteristic feature of the megaspores is the high, blade-like commissural ridges.

Of the various species of *Isoetes* reported by Pfeiffer (1922) from the eastern half of North America, only *I. melanopoda* has megaspores as small as the ones

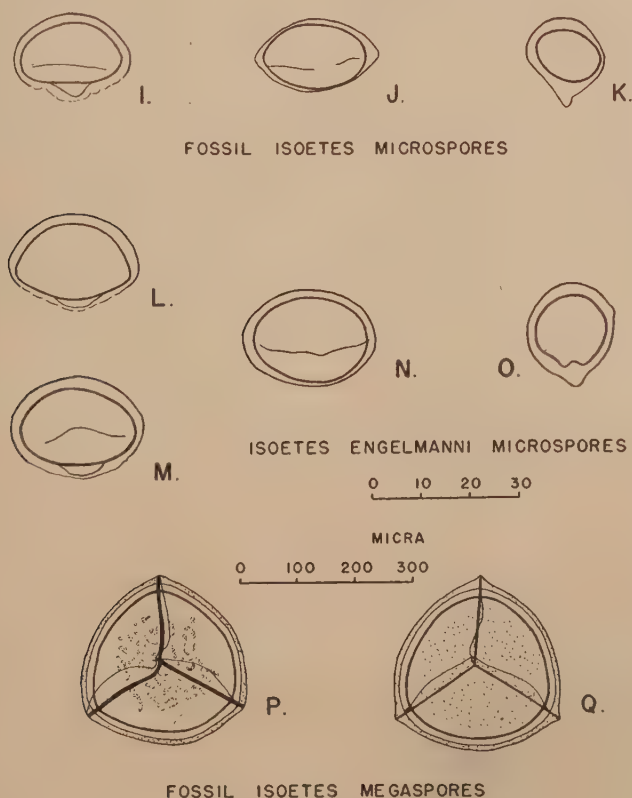


FIG. 6. Camera lucida sketches of *Isoetes* microspores and megaspores: I, J, and K—fossil microspores, Si-25, 13.75 ft.; L, M, N, and O—fresh microspores of *I. Engelmanni* from North Carolina; P—fossil megaspore with distal rugae, Si-25, 16.25 ft.; Q—fossil megaspore, smooth, Si-25, 16.0 ft.

found in the sediments, but this species now occurs only in the mid-continental region and its microspores are described as fine spinulose. *I. Engelmanni*, which is the common species in North Carolina at present, has much larger megaspores (400 to 570 μ) with a distinct honeycomb surface pattern, and its microspores although mostly smooth are significantly larger than the fossil spores. One hundred grains averaged $26.2 \pm 0.15 \mu$ in size, and ranged from 23 to 30 μ . *I. lithophila* from Texas has smooth to slightly ridged megaspores of the proper size with high, narrow commissural ridges, but its microspores are all 30 μ or larger. The small dimensions of the fossil material may be another example of the suggested tendency previously noted for fossil pollen (and spores?) to lose part of their ability to expand in aqueous media.

No attempts were made to distinguish between the various species of oaks and hickories. Other types of pollen likewise, particularly the non-arboreal types, were lumped into the larger groups that are easy to recognize on the basis of their pollen morphology.

SUMMARY

The Carolina bays, as judged by the sediments in Singletary Lake, are evidently much older than previously believed. A pine-spruce maximum, representing the Mankato maximum, occurs well near the top of the sediments in the lake proper. The radiocarbon age of the hemlock-beech-hickory-oak maximum a short distance above the pine-spruce maximum is $10,224 \pm 510$ years.

Below the pine-spruce maximum are two organic layers, each showing an amelioration of climate. The minimum radiocarbon age of each of these layers is greater than 20,000 years, which according to the present-day interpretation antedates the Cary-Mankato interval. It is not believed, however, that either of these layers breaks through into the Sangamon because of the almost continuous presence

of spruce pollen in the sediments. Assuming constant rates of sedimentation, the age of the lowermost sediments is calculated to be between 40,000 and 100,000 years.

Above the pine-spruce maximum the climatic shift was immediately to warm, moist, indicated by maxima of hemlock and beech; then to warm, dry, represented by a pronounced oak maximum; and finally to a moister climate again, as shown by various peaks of cypress, tupelo, and *Sphagnum*. These post-Mankato changes in vegetation and the climatic conditions they indicate are similar to those already known from northeastern North America, although the lowermost deciduous zone was almost certainly of greater duration than its northern equivalent.

The size-frequency distribution of pine pollen exhibits extensive and regular changes from one level to another, representing changes in species composition during the various climatic periods. The species present could not be identified on the basis of the size-frequency characteristics of extant populations. Two species of spruce appear to be present, *P. glauca* and *P. mariana*, with the former more abundant. *Isoetes* microspores were the most abundant of all plant remains. The species could not be definitely identified, except that it does not appear to be *I. Engelmanni*, the species widespread in North Carolina at present.

In a basin as shallow as that of Singletary Lake one might expect the bottom sediments to have been disturbed in their long history by the activities of organisms and perhaps also by periods of erosion and re-deposition. It is quite certain that the post-Mankato sediments have not been reworked. Sediments representing pre-Mankato time may have been reworked to a limited extent, although such activity is not evident from the pollen diagrams.

In contrast to more northern basins that have been studied, the rate of sedimentation in Singletary Lake has been very slow. In the past 10,000 years at site Si-25, sediments have accumulated

at the average rate of only one inch every 730 years.

BIBLIOGRAPHY

- Arnold, J. R., and W. F. Libby.** 1951. Radiocarbon dates. *Science*, **113**: 111-120.
- Buell, M. F.** 1945. Late Pleistocene forests of southeastern North Carolina. *Torrey*, **45**: 117-118.
- . 1946. A size-frequency study of *Pinus banksiana* pollen. *Jour. Elisha Mitchell Scient. Soc.*, **62**: 211-228.
- Cain, S. A.** 1940. The identification of species in fossil pollen of *Pinus* by size-frequency distribution. *Amer. J. Bot.* **27**: 301-308.
- . 1944. Pollen analysis of some buried soils, Spartanburg County, South Carolina. *Bull. Torrey Bot. Club*, **71**: 11-22.
- . 1948. Palynological studies at Sodon Lake. I. Size-frequency study of fossil spruce pollen. *Science*, **108**: 115-117.
- Cain, S. A., and L. G. Cain.** 1948a. Palynological studies at Sodon Lake. II. Size-frequency studies of pine pollen, fossil and modern. *Amer. J. Bot.*, **35**: 583-591.
- . 1948b. Size-frequency characteristics of *Pinus echinata* pollen. *Bot. Gaz.*, **110**: 325-330.
- Cocke, E. C., I. F. Lewis, and Ruth Patrick.** 1934. A further study of Dismal Swamp peat. *Amer. J. Bot.*, **21**: 374-395.
- Darlington, H. C.** 1943. Vegetation and substrate of Cranberry Glades, West Virginia. *Bot. Gaz.*, **104**: 371-393.
- Davis, J. H.** 1946. The peat deposits of Florida. *Fla. Dept. Conserv., Fla. Geol. Surv., Geol. Bull.* **30**. xiv + 247 pp.
- Deevey, E. S., Jr.** 1949. Biogeography of the Pleistocene. *Bull. Geol. Soc. Amer.*, **60**: 1315-1416.
- . 1951. Late-glacial and postglacial pollen diagrams from Maine. *Amer. J. Sci.*, **249**: 177-207.
- Flint, R. F., and E. S. Deevey, Jr.** 1951. Radiocarbon dating of late-Pleistocene events. *Amer. J. Sci.*, **249**: 257-300.
- Frey, D. G.** 1949. Morphometry and hydrography of some natural lakes of the North Carolina Coastal Plain: the bay lake as a morphometric type. *Jour. Elisha Mitchell Scient. Soc.*, **65**: 1-37.
- . 1950. Carolina bays in relation to the North Carolina Coastal Plain. *Jour. Elisha Mitchell Scient. Soc.*, **66**: 44-52.
- Knox, A. S.** 1942. The use of bromoform in the separation of non-calcareous microfossils. *Science*, **95**: 307-308.
- Lewis, I. F., and E. C. Cocke.** 1929. Pollen analysis of Dismal Swamp peat. *Jour. Elisha Mitchell Scient. Soc.*, **45**: 37-58.
- Oberdorfer, Erich.** 1931. Die postglaziale Klima- und Vegetationsgeschichte des Schluchsees (Schwarzwald). *Ber. Nat. Ges. Freiburg i. Br.*, **31**: 1-85.
- Pfeiffer, N. E.** 1922. Monograph of the Isoetaceae. *Ann. Missouri Bot. Garden*, **9**: 79-232.
- Potzger, J. E.** 1945. The pine barrens of New Jersey, a refugium during Pleistocene times. *Butler Univ. Bot. Stud.*, **7**: 182-193.
- Potzger, J. E., and C. C. Tharp.** 1947. Pollen profile from a Texas bog. *Ecology*, **28**: 274-280.
- Radford, A. E.** 1950. Notes on *Isoetes* in North Carolina. *Jour. Elisha Mitchell Scient. Soc.*, **66**: 84-86.
- Sears, P. B.** 1935. Types of North American pollen profiles. *Ecology*, **16**: 488-499.
- Wilson, I. T.** 1941. A new device for sampling lake sediments. *Jour. Sedimentary Petrology*, **11**: 73-79.

NOTES AND COMMENT

THE STIMULATIVE EFFECT OF FIRE ON THE FLOWERING OF THE GOLDEN BRODIAEA (*BRODIAEA IXIOIDES* WATS. VAR. *LUGENS* JEPS.)¹

During a plant physiological study of some of the species making up the southern California brush fields it was noted that following a fire many areas are blanketed by the yellow blooms of the golden brodiaea. Previous workers have reported a tremendous increase in the seed germination of both brush and annual species at such times (Wright 1931, Quick 1935, Samson 1944), and, in one instance, it was shown to be the result of heat stimulation (Stone and Juhren 1951). However, increased flowering of the brodiaea could not have resulted from stimulated seed germination since it takes several years for a flowering plant to develop from seed. In other areas it has been found that the blooming of some grasses are stimulated by fire primarily through the removal of old foliage (Burton 1944, Curtis and Partch 1950). Again this does not explain the results obtained with brodiaea since there is no residual basal tuft of foliage; instead the one leaf formed per year dries up and falls off during the summer months. Therefore the study here reported seemed worth while and was set up to determine, if possible, how burning stimulated the flowering of such a plant as the brodiaea.

METHODS AND RESULTS

This study can be divided into two parts. The first consisted of field observation and experimentation. The second consisted of a greenhouse study where the variable factors of light, temperature, and moisture were controlled.

Field study

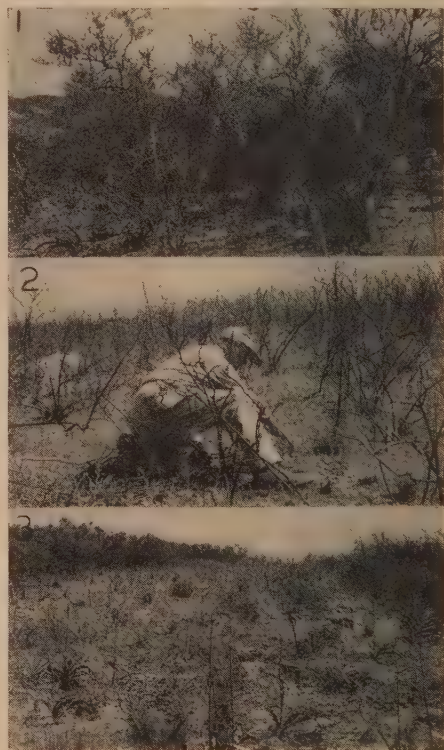
This study was started in January following an October 1948 fire in Topanga Canyon, Los Angeles County, California. Most of the ground cover in the canyon had been burned. However, there were isolated areas, several acres in extent, which had been skipped by the fire. This made possible the comparison of burned and unburned plots within a few feet of each other.

Five one-hundred-square-foot plots were laid out in adjacent burned and unburned areas (Figs. 1, and 2). In addition approximately an acre of the unburned brush was removed and five additional plots laid out in this area (Fig. 3). A 10 per cent sample of each plot was taken by running a transect, made up of ten one-square-foot plots, through the middle of each one. The

slope of the plots varied from 2-20 per cent and the aspect was northerly.

Observations on the number of golden brodiaea plants as well as those in flower were made on the first of each month starting in January and ending in July. A summary of these data are presented in Table I. Although some plants of *Brodiaea capitata* Benth. were included in these observations, since they are indistinguishable by vegetative characteristics, there were so few in the area that the error involved was small.

Several facts are readily apparent from the data.



FIGS. 1-3. Pictures taken in February to show the conditions existing under the three different treatments. Brodiaea plants do not show up since at this date they consist of one leaf 1 to 6 inches long. Fig. 1. Uncleared brush stand. Fig. 2. Brush burned. Fig. 3. Brush cleared.

¹ Part of this work was carried out when the author was a member of the staff of the Calif. Forest and Range Exper. Station, San Dimas, California.



FIG. 4. Flowering of *Brodiaea ixioides* in the greenhouse as affected by different degrees of shade. Light values in foot-candles, from left to right are: 6,500, 1,000, 500, 250, 100, and 50.

(1) The number of brodiaea plants per square foot is extremely variable but not greatly different in the burned, unburned, and cleared areas.

(2) Removal of the brush cover by fire results in flowering.

(3) Removal of the brush cover by clearing also results in flowering.

These facts would suggest that the most probable effect of fire is not through the addition of ash or through heat stimulation but rather the removal of shade.

TABLE I. *The effect of burning and clearing on the flowering of Brodiaea ixioides on fifteen one-hundred-square-foot plots*

Plot	Treatment	No. of plants per sq. foot		No. of plants flowering per sq. foot	
		Average	Range	Average	Range
1	Burned	3.0	0-6	3.0	0-6
2	Burned	2.4	0-4	2.4	0-4
3	Burned	3.0	0-5	2.8	0-4
4	Burned	2.2	0-4	2.2	0-4
5	Burned	0.4	0-2	0.2	0-1
Average per treatment		2.5		2.3	
6	Cleared	4.4	2-8	4.0	1-5
7	Cleared	3.6	3-6	2.8	0-4
8	Cleared	0.0	0-0	0.0	0-0
9	Cleared	1.6	0-3	0.4	0-2
10	Cleared	2.3	0-5	2.3	0-5
Average per treatment		2.4		1.9	
11	Untreated	0.8	0-2	0.0	0-0
12	Untreated	0.0	0-0	0.0	0-0
13	Untreated	3.0	0-4	0.0	0-0
14	Untreated	2.4	0-3	0.0	0-0
15	Untreated	3.6	1-5	0.0	0-0
Average per treatment		2.0		0.0	

TABLE II. *Light intensities under frames at noon on an average clear day*

Frame no.	Layers of mosquito netting	Average light intensities (foot-candles)
1	0	6,500
2	1	1,000
3	2	500
4	3	250
5	4	100
6	5	50

Although these field observations were certainly indicative, the variable factors of temperature and moisture could not be ruled out. Therefore, rather than conduct extensive field measurements on light intensities, air temperature, soil temperatures, and soil moisture content and then hope to discover some correlation, it was decided to grow these plants in the greenhouse where these otherwise variable factors could be controlled.

Greenhouse studies

Several hundred bulbs were dug during July 1949 and placed in storage at room temperature. In October, ninety of these bulbs were stratified in damp peat moss and held for three months at 5° C. Then in January these and another ninety unstratified bulbs were planted in sandy loam contained in gallon cans. Each can was planted with three bulbs at a depth of three inches. Six different degrees of shade were obtained by using 3' × 4' × 6' frames covered with either 0, 1, 2, 3, 4, or 5 layers of olive drab army mosquito netting. The light intensities under each degree of shade were measured with a Weston model 603 exposure meter and are shown for an average clear day at noon in Table II. Five cans (15 bulbs) of stratified

and five cans of unstratified bulbs were placed under each frame, kept well watered and their growth and flowering noted.

The number flowering per can, per treatment, as well as the days to flowering is shown in Table III. Figure 4 shows representative samples from each of the shade treatments. No difference was noted between stratified and unstratified bulbs.

Several conclusions can be drawn from the data in Table III.

(1) One layer of netting which reduced the light intensity to 1,000 foot-candles does not influence the number of plants blooming but does cause them to flower later.

(2) Two layers of netting which reduced the light intensity to 500 foot-candles did not significantly reduce the number of plants which flowered, but did result in a more spindly inflorescence and also caused still later flowering.

(3) Three layers of netting which reduced the light intensity to 250 foot-candles entirely prevented flowering. These data thus substantiate the conclusions from field observations, namely that light intensity is the factor controlling flowering before and after a burn.

DISCUSSION

The combination of greenhouse and field data definitely point to shade-removal as being the factor responsible for the flowering of the golden brodiaea after a fire. However, the threshold light intensity value for flowering in the field was not determined. Although 500 foot-candles would just barely permit flowering in the greenhouse it delayed the time of flowering as much as three months. Under such a low light intensity in the field soil moisture might well become limiting before flowering could occur. However, we can say that a brush cover with a

TABLE III. *Number and time of flowering of plants of Brodiaea ixioides under different degrees of shade*

Treatment	No. of layers of mosquito netting	Average illumination at noon (foot-candles)	Plants flowering per can		Avg. no. of days to flowering
			Avg.	Range	
Unstratified	0	6,500	2.7	2-3	90
Unstratified	1	1,000	2.0	1-3	120
Unstratified	2	500	2.3	1-3	180
Unstratified	3	250	0.0	0-0	—
Unstratified	4	100	0.0	0-0	—
Unstratified	5	50	0.0	0-0	—
Stratified	0	6,500	3.0	3-3	80
Stratified	1	1,000	2.7	2-3	135
Stratified	2	500	1.7	1-3	180
Stratified	3	250	0.0	0-0	—
Stratified	4	100	0.0	0-0	—
Stratified	5	50	0.0	0-0	—

density such that the light intensity is 250 foot-candles or less will not permit flowering.

Apparently within the mature brush stands brodiaea grows year after year without blooming. The light intensity is high enough to permit the continued growth of the plant but not high enough to permit blooming. After a fire the shade is removed and the plant is able to flower. It appears that yearly flowering then continues until the brush stand again becomes dense enough to reduce appreciably the light intensity beneath it.

SUMMARY

1. The effect of fire on the flowering of brodiaea was apparently exerted through the removal of shade.

2. Removal of shade in the field by mechanical clearing of the brush cover was just as effective as fire.

3. In the greenhouse, flowering can also be controlled by manipulating the light intensities. Below a light intensity of 500 foot-candles (two layers of mosquito netting) flowering was prevented; while above this light intensity flowering occurred.

LITERATURE CITED

- Burton, G. W. 1944. Seed production of several southern grasses as influenced by burning and fertilization. *Jour. Amer. Soc. Agron.* 36: 523-529.
- Curtis, J. T., and M. L. Partch. 1950. Some factors affecting flower production in *Andropogon gerardi*. *Ecology* 31: 488-489.
- Quick, C. R. 1935. Notes on the germination of *Ceanothus* seeds. *Madroña* 3: 135-139.
- Sampson, A. W. 1944. Plant succession on burned chaparral lands of northern California. *California Agr. Exper. Sta. Bull.* 635: 1-144.
- Stone, E. C., and G. Juhren. 1951. The effect of fire on the germination of the seed of *Rhus ovata* Wats. *Amer. Jour. Bot.* 38: in press.
- Wright, E. 1931. The effect of high temperatures on seed germination. *Jour. Forestry* 29: 679-687.

E. C. STONE

SCHOOL OF FORESTRY,
UNIVERSITY OF CALIFORNIA,
BERKELEY 4, CALIFORNIA

OUTLINE FOR AN ECOLOGICAL LIFE HISTORY OF POCKET GOPHERS AND OTHER FOSSORIAL MAMMALS

INTRODUCTION

Pocket gophers are a family (Geomyidae) of fossorial rodents that have external, fur-lined cheek pouches; short, stout legs with large claws on the forefeet; and small eyes and ears. They are seldom seen above ground and often known to be present only through the small mounds of earth brought to the surface by their excavations. Even though their damage to gardens and agricultural crops is well known (Crouch 1942; Lantz 1918; Scheffer 1931), more ecological life history studies are essential to the proper understanding of these animals and to their control, when such is deemed necessary (Taylor 1948).

The object of this outline is to stimulate investigators to obtain as thorough a knowledge as is possible of the ecological life history of these mammals. It is not an exhaustive tabulation of all the problems and the methods by which such studies can be made, but is intended to expedite investigations by suggesting a number of problems for study and also by listing methods that have been tried and proved successful.

In North America there are three genera of pocket gophers. The western pocket gopher (*Thomomys*) occurs over most of western North America. The eastern pocket gopher

(*Geomys*) is found on the plains and prairies from the eastern foothills of the Rocky Mountains and the Mississippi River to the eastern Gulf States. The Mississippi pocket gopher (*Cratogeomys*) occurs through most of the Mississippi Valley.

Although this outline is based primarily on study of *Thomomys*, it should apply equally well to other members of the family Geomyidae. Much of it will pertain also to other fossorial rodents, such as those of the Old World families Spalacidae, Bathyergidae, and Rhizomyidae, and the South American Ctenomyidae and Octodontidae, which parallel the North American pocket gophers to a remarkable degree although they are not closely related to them. In a lesser degree it will serve for fossorial mammals of other orders (such as moles) and for small rodents in general.

For a more complete understanding of how various environmental factors may influence pocket gophers, the animals should be studied throughout the entire range of biotic communities inhabited, both on areas little disturbed by man and on others greatly altered by agricultural practices.

Live trapping and releasing of marked pocket gophers will provide information about individuals of a natural population with regard to their

growth rate, molt, reproduction, movements, population structure, home range, seasons of activity, soil moisture and temperature preferences, parasites and diseases, co-inhabitants of their burrow systems, and many other environmental responses. Even though re-trapping live animals which have been released provides the greatest amount of data, the kill trapping of pocket gophers may be valuable in an ecological life history study, because a greater number of individuals can be procured with less effort. Freshly killed gophers provide quantitative data on stomach and cheek pouch contents, parasites and diseases, taxonomy, distribution, reproduction, and other subjects.

In addition to studying pocket gophers in the wild, an ecological life history can be augmented by keeping live animals under observation in a laboratory. It is particularly difficult to learn much about the daily activity of pocket gophers under field conditions because the animals live almost exclusively below ground. Studies of caged gophers, however, enable the investigator to learn much of their behavior, which makes it possible for him to design better field experiments. Laboratory studies permit efficient handling of large numbers of individuals and provide a control over certain environmental factors. One must never lose sight of the fact, however, that wild animals may not display normal responses when placed in captivity, and final determination of behavior patterns and other life history phenomena should be confirmed under field conditions.

Acknowledgments are due Henry S. Fitch, Milton A. Miller, and Tracy I. Storer for critically reading the manuscript.

METHODS

Marking

Toe clipping has proved a successful means of marking live trapped pocket gophers. One or two toes may be removed from each foot. It is not advisable to cut any of the three middle toes on the fore feet, because they are the principal toes used in digging and fighting. (Mistakes in reading the clipped toes are easily made and should be guarded against by two or more readings before the animal is released.)

Trapping

The traps must be buried within the burrow rather than placed at random on top of the ground as is done with many other kinds of small mammals. The burrow system of a pocket gopher is readily determined, however, by the conspicuous mounds of fresh earth pushed up to the surface from the subterranean tunnels. Active runways are located by probing with a short piece of stiff wire near mounds of fresh earth.

After a field plot has been selected, stake it in

a grid pattern of 20-foot spacing; number one co-ordinate and letter the other to facilitate recording exact locations. Since pocket gophers alter their burrow systems, fixed trapping stations cannot be established as is commonly done in studies of other small rodents.

Effective live traps have been designed by Howard (MS), Ingles (1949c), Scheffer (1934), and Sherman (1941). The traps have wire bottoms (the Ingles and Scheffer models are cylinders of hardware cloth) to permit dirt to sift through. If a small hole is left uncovered at the rear of the trap no bait is required; however, it is better to add rolled oats or other food to keep the animals in better condition after being trapped. During cold weather gophers will die when confined in traps unless food is provided (Howard 1951). Live traps can be left set day and night. During hot weather they must be covered with ample dirt or set only at night. Set traps may be profitably examined in the morning, near midday, again late in the afternoon, and if convenient, during the night. Individuals are often caught within less than one hour after a trap is set. To determine whether more than one gopher is living in a runway, more than one trap can be set side by side in the same hole. Two adults are seldom caught in the same burrow system and adults usually cannot be caged together without fighting. The larger animal, irrespective of sex, usually kills the smaller.

Two or more kill traps set in the same runway will provide information on multiple occupancy of a burrow system. There are many types of commercial kill traps available but most of them are modifications of the yet unsurpassed Macabee style of trap.

Cages

When pocket gophers are placed in dirt-filled cages (either vertical with glass sides or horizontal with a glass top), they excavate burrow systems but still remain visible to the investigator. When not under observation, cardboard should be placed over the glass to keep the burrows in darkness. Under glass, information can be acquired regarding their digging, fighting, feeding, storing of food, reactions to enemies, responses to water in burrow, reaction to other gophers, family life, mannerisms, sanitation, daily activity, nests, responses to soils of varying temperature and moisture conditions, preferences for different soil types, taste, smell, hearing, and tactile hairs.

Gophers can also be housed in open-top cages with sheet metal sides approximately twelve inches high. Another type of cage was described by Sherman and Barrington (1941). Gophers can be picked up by their tails without the investigator being bitten. The caged animals remain in better condition if some soil is

provided. If given only dry food, they should be provided with drinking water, but free water is not required when they live in earthen burrows in the laboratory. Pocket gophers lend themselves well as laboratory animals for experiments that require frequent handling. They tame quickly if handled gently. Known amounts and kinds of food can be fed captives and their droppings and stomach contents analyzed to verify field findings of food habits. The reproductive cycle, gestation period (from field-caught females, as pocket gophers have not been bred in captivity), age-size relationships, acceptability of different baits, and susceptibility to different poisons, can largely be determined from caged animals.

Records

It is desirable to have access to daily weather records from the nearest weather station. Detailed maps of study area which show vegetative types and physiographic features should be made if not available. Take photographs of all phases of the work as records and as illustrations for publications. Determine the reliability of: placental scars for determining litter size and total offspring; weight as a criterion for age; contents of cheek pouches, stomachs, and feces for information about feeding habits; and population indices, such as mound counts and strip counts in estimating population density (Ingles *et al.* 1949).

A running account of general comments can be kept in a field notebook. Separate sheets or cards should be maintained for each live trapped animal. Five by eight inch cards serve well for individual records as they can be punched and carried in a field notebook and are easy to shuffle when analyzing the data. An outline can be printed on cards used for kill trapped individuals to save time when entering data and to ensure that all necessary items are recorded from each animal.

Every time a marked animal is recaptured it should be checked against its past history before being released; otherwise important information may later be of questionable reliability because of error in identification of the animal by reading the clipped toes wrongly. Additional features such as scars, broken tails, and maimed legs should also be recorded to help verify subsequent identification. Sex and weight are often important identifying characteristics and both should be noted each time an individual is trapped.

When a gopher is live or kill trapped some or all of the following items should be recorded: date; hour; location; sex; estimated age as to whether immature, young, subadult, or adult; body weight; breeding condition; and whether pubic symphysis is open or closed in females (determined by pressing a finger over the pubic re-

gion). The pubic symphysis is absorbed under the influence of ovarian hormones during pregnancy (Hisaw 1925).

Mammals in general have been called adults when they are either a prescribed number of days old, possess adult pelage, or have become sexually mature. With pocket gophers the following definitions of age classes have proved workable. An adult has adult pelage or at some time has attained sexual maturity even if not at that moment in breeding condition. A subadult has subadult pelage and has not attained puberty. A young gopher has hair, eyes are open, is immature sexually, is under parental care, and may or may not be still nursing. An immature gopher is hairless, eyes are closed, is confined to the nest, and feeds exclusively on its mother's milk.

The breeding condition is difficult to determine during the non-breeding season unless the penis is extruded on males or the pubic symphysis is open or the teats are large on females. When recording data on breeding condition of females many of the following should be recorded: vulva swollen or not swollen, imperforate or perforated; vaginal smear to determine stage in estrus cycle; diameter, turgidity, and blood supply of uterus; number and size of embryos; condition of ovaries (clear follicles, corporal lutea, etc.); number of placental scars; number and size of teats; and whether lactating as determined by milking teats with forceps. With males note: position, size, weight, color, and turgidity of testes; maximum diameter of seminal vesicles and cauda epididymis; presence of motile sperm; and conspicuousness of reproductive vascular supply.

Field equipment

The type of study undertaken will determine the kind of equipment necessary, but the following list may be helpful: a light, sturdy, short-handled shovel or a small hand mattock for setting live traps and for excavating burrows; wire stakes, long enough to project well above the tallest vegetation, with a colored rag or other marker tied at the top to show trap locations; wooden stakes numbered on one side and lettered on the other to grid a study plot; a carrying crate to hold traps, stakes, and bait; a piece of heavy wire about one foot long as a probe for locating runways; a caliper to measure the internal diameters of burrows (which then may be compared to the weights of animals caught in the same tunnels); thermometers; a dietary balance for rapidly recording live or dead weights of the animals (live pocket gophers will usually remain quietly on the scale pan); a wire "holding sock" or/and thick all-leather gloves for handling live gophers; rubber tipped, 12-inch forceps or kitchen tongs to help catch escaped captives; dissecting scissors or cuticle

clippers to clip toes when marking live individuals; small forceps for removing food from cheek pouches, collecting parasites, and other purposes; and rolled oats (wheat or barley) as bait.

SUGGESTED PROBLEMS

A number of important problems regarding various aspects of pocket gophers, which are in need of further investigation, are suggested below under various sub-headings in the form of incomplete sentences and phrases. Most of the references cited pertain to more than one sub-topic, but usually are listed only once to save space.

The immature and young

Size at birth (Barrington 1942; Hill 1934; Wight 1918), sex ratio, growth rate (Sagal 1942), weight (Ingles 1949a), body dimensions, opening of eyes, appearance of hair, and molts. Number of young per litter in relation to season, elevation, geographic location, food, and age and size of mother (Aldous 1935; Bond 1946; Horn 1923; Miller 1946; Scheffer 1938; Wood 1949). Association with male parent. Evidence of embryo absorption (Miller 1946) or destruction of young by female parent (Johnson 1926). Age at time of first leaving nest, of weaning, of first appearing above ground (Burt 1933), and of earliest plant feeding. Mortality rate in relation to sex and age. Parasites and diseases acquired from parents.

The subadult

Reliability of weight as a criterion of age classification between subadults and adults. Rate of growth of subadults. Age at sexual maturity depending upon season when born. Amount of digging, if any, before leaving parental burrow. Age when leave home (disperse) with reference to sex, season when born, and attainment of puberty (Howell 1922). Occurrence of dispersing above ground (Bryant 1913; Imler 1945). Factors that cause them to leave the home burrow. Compatibility with parents and each other at the time when leaving home. Percentage of subadults of both sexes that succeed in establishing burrow systems.

The adult

Physical characteristics. Weight of both sexes (Smith 1940) at different ages to determine whether adult males continue to grow more than adult females. Ways in which gophers are physically adapted to a fossorial existence (Hill 1937; Holliger 1916). Sounds, vocal and mechanical, and their functions (Wight 1918). Means of communication between neighboring individuals. Keenness of senses of smell and taste. Tactile functions of the fibrissae and tip of tail on fossorial animals. Speed of travel, both frontwards and backwards, within bur-

rows. Comparison of life expectancy of the mature and established pocket gopher to that of non-fossorial small rodents. (The evidence suggests that the incidence of natural mortality of established gophers is low.)

Growth. Factors that initiate and terminate breeding (Dixon 1929). Duration of gestation and lactation. Continuous growth rate of incisors. Correlation between growth rate of the claws on different toes in relation to degree of use in digging. Relation of body size to soil and altitude (Davis 1938, 1939; Hall 1946). Number and progression of molts and individual variations in molt stages (Bailey 1915). Seasonal differences in length and color of hairs. Correlation of pelage color with elevation, weather, color of soil (Benson, 1933; Goldman 1947), vegetative cover, and inheritance (Storer and Gregory 1934). Age at time adult pelage is acquired, depending on season when born.

Social habits. Compatibility between adult males, adult females, and adult males and adult females depending on season and breeding. Relationship between occupants of adjacent burrow systems. Methods by which each sex determines the other's receptivity. Which sex seeks the other for breeding (Wight 1930) and length of time they remain together. Occurrence of monogamy, promiscuity, or polygamy. Relation of males to family life.

Feeding. Different age and seasonal preferences for certain foods. Relation of food preferences to growth and reproduction. Kind and quantity of food eaten (Aldous 1951; Wade 1927; Wight 1918) and cached (Aldous 1945). Manner in which gophers handle bulbs, carrots, and other large vegetables before the materials are cached (Miller and Howard 1951). Arrangement of food caches and the presence of earthen plugs in tunnels between food stores and the rest of the burrows. Time of day and season when the animals feed and the amount of food acquired from above ground (Bryant 1913). Relation between animal weights and amount and quality of surface vegetation available. Density of population depending on food supply. Manner in which grazing and other agricultural practices affect gophers by changing kind and amount of food available. Analysis of contents of cheek pouches, stomachs, and feces to determine feeding habits. Use made of furred cheek pouches (Merriam 1895).

Daily and seasonal activity. Correlation of activity to time of day or night (Tryon 1947). Effects of light, temperature, moisture, vegetative cover, and reproduction on daily cycles of activity. Differences in time of activity of young and subadults to that of adults. Relation of seasonal activity to weather and food supply. Occurrence of seasonal migrations (Ingles 1949b). Occurrence of estivation in localities where herbaceous vegetation and soil become

dry during the summer. Occurrence of hibernation or short periods of torpidity during winter. Significance of the sound sleeping habit in gophers (English 1932). Effect of frozen ground.

The population. Percentage of population that consist of young, subadults, adult females, and adult males at various seasons. Principal factors causing mortality of the different age classes. Life span of both sexes and evidence of senility. Selection of home ranges by subadults and the movements of adults to new home sites (Wight 1930). (It appears better to express home range as length of longest distance between mounds or trap sites rather than as an area.) Extent of burrow system (home range) an adult defends (territory) from other gophers. Fluctuations and cycles in population density. The minimum composition of a breeding population. Rate of recovery of a population of gophers after they have been trapped or poisoned. Statistically significant differences of population structure in different habitats. Frequency and maximum distance individuals disperse at different ages. Barriers to dispersal (Dalquest and Scheffer 1944). Effect of dispersals on genetic composition of a population and amount of inbreeding occurring. Intergradation, if any, between adjacent local or geographic races (Villa-R and Hall 1947).

Predators. Little is known on how the principal predators (Criddle 1930; Evans and Emelen 1947; Hisaw and Gloyd 1926; Tryon 1943) take gophers. Presumably a greater proportion of young and subadult gophers than adults are taken by the predators than is the case with most other small rodents. Hawks and owls probably swoop down on gophers as they are dispersing or venturing from their burrow to feed on surface vegetation or to deposit excavated earth. Rattlesnakes and possibly other predators may wait beside burrow entrances. Bullsnares and other small predators may pursue gophers underground, but it is questionable whether they are able to catch many adults in the burrows. Vulnerability to predators in relation to weather conditions, particularly following heavy rains that may flood their burrows. Escape reactions, such as depositing dirt at ground surface under shelter of brush when available, ability to plug runways when pursued by a snake or weasel, foraging at night, and dispersing in cover of darkness. Age and seasonal differential in vulnerability of gophers. Age and sex classes recovered from pellets and droppings of predators (Tryon 1947). Effect of the control of gophers on their predators.

Parasites and commensals. Kinds of parasites and commensals represented and seasonal variations in occurrence. Behavior traits of the gophers which favor the incidence of parasites. Evidences of disease organisms that affect

gophers (also man and domestic animals) in populations living under natural conditions. Other small animals that inhabit the burrows and nests of gophers (Chamberlain 1943; Hubbel and Goff 1939). Way new burrow systems acquire nest-living commensals.

Burrow systems

The physical burrow. Methods of excavation by the animals (Breckenridge 1929). Frequency, amount, and rate (Mohr and Mohr 1936) animals dig. Length and pattern of burrow systems (Hall 1946; Scheffer 1940; Storer 1949). Amount of digging without bringing excavated dirt above ground by establishing new tunnels and plugging others. Frequency and purpose of deep vertical tunnels. Extent to which main runways and laterals are used. Correlation between burrow diameter and weight of occupant. Importance of plugging as a means of escaping hostility of other gophers, of blocking off invading predators, of disposing of excavated earth without risk involved in carrying it to surface.

Nests. Number (Scheffer 1940), size, and use of nests. Relation between their depth below the ground surface (Wight 1930) and the temperature and moisture content of the soil. Materials used in nest construction. Similarity of those made in the snow to subterranean nests. Determine whether nests are made from inedible remains of food plants or from other materials. Location of nests with respect to protection from predators. Number of entrances. Sanitation in nest and burrow.

Effect of environment. Degree to which depth and length of burrow are determined by the depth and type of soil, available food, age of burrow, level of water table, snowfall (Ingles 1949b; Marshall 1941) and sex and age of occupant. Relation of digging activity to soil moisture and temperature (Miller 1948). Compare burrow temperatures with that of soil at similar depths. Soil types preferred and avoided with respect to workability (amount of rock and compactness), amount of organic matter, drainage, and depth. Vegetation on preferred habitats. Preference for light or shaded areas. Lethal effects of natural soils with a high content of toxic substances. Soil moisture as a factor in distribution. Relation of range and distribution to food, soil conditions (Davis *et al.* 1938; Grinnell 1926), altitude, slope, rainfall, snowfall, and temperature. Influence of grazing or other agricultural practices on population density (Dixon 1922; Buechner 1942). Effect of cultivation and irrigation on gophers.

Effect on environment. Evidence that gopher diggings drain soil that otherwise would be too wet for grasses. Effect of diggings on the infiltration of water (Grinnell and Storer 1924). Degree of slope where subsurface runoff is

channeled through gopher runways, and the frequency such channeling results in a cave-in of the ground surface. Relationships of pocket gophers to the construction of mima mounds, pimple mounds, and "hog wallows" (Arkley 1948; Dalquest and Scheffer 1942; Kelley 1948; Larrison 1942; Price 1949; Scheffer 1947; Stallings 1948). Relation of burrowing and the deposition of mounds of earth on ground surface to forage yield (Larrison 1942). The degree of reduction of range vegetation, which would otherwise be available to livestock, by gophers foraging for food and covering vegetation with dirt (Buechner 1942; Fitch and Bentley 1949). Alteration of plant composition by gophers on range lands (Cook 1939). Comparative values of soil "cultivation" by plant roots and microorganisms to that done by gophers (Dice 1939; Grinnell 1923; Scheffer 1948). Relation of gopher diggings to rates of soil erosion (Ellison 1946; Gabrielson 1938), organic matter in soil (Taylor 1935), and soil profiles.

Degree to which other small mammals use pocket gopher burrows while gophers are still present and after they have died (Scheffer 1945). Dependence of thin-skinned amphibians such as *Ambystoma* (Warren 1937), *Scaphiopus*, and *Ensatina* on the humid atmosphere of gopher burrows. Dependence of various snakes and lizards on the burrows for sites sufficiently humid for the eggs to escape destruction. Use that subterranean arthropods make of gopher burrows. Degree to which gophers are hostile or tolerant of the different kinds of burrow associates.

LITERATURE CITED

- Aldous, C. M. 1945. Pocket gopher food caches in central Utah. *Jour. Wildlife Management*, 9: 327-328.
- . 1951. The feeding habits of pocket gophers (*Thomomys talpoides moorei*) in the high mountain ranges of central Utah. *Jour. Mamm.*, 32: 84-87.
- Aldous, Shaler E. 1935. Some breeding notes on rodents. *Jour. Mamm.*, 16: 129-131.
- Arkley, Rodney J. 1948. The mima mounds. *Scientific Monthly*, 66: 175-176.
- Bailey, Vernon. 1915. Revision of the pocket gophers of the genus *Thomomys*. U.S.D.A., Bur. Biol. Survey, N. Amer. Fauna, No. 39. 136 pp.
- Barrington, B. A., Jr. 1942. Description of birth and young of the pocket gopher, *Geomys floridanus*. *Jour. Mamm.*, 23: 428-430.
- Benson, Seth B. 1933. Concealing coloration among some desert rodents of the southwestern United States. *Univ. Calif. Publ. Zool.*, 40: 1-70.
- Bond, R. M. 1946. Breeding habits of *Thomomys bottae* in Orange County, California. *Jour. Mamm.*, 27: 172-174.
- Breckenridge, W. J. 1929. Actions of the pocket gopher (*Geomys bursarius*). *Jour. Mamm.*, 10: 336-339.
- Bryant, H. C. 1913. Nocturnal wanderings of the California pocket gopher. *Univ. Calif. Publ. Zool.*, 12: 25-29.
- Buechner, H. K. 1942. Interrelationships between the pocket gopher and land use. *Jour. Mamm.*, 23: 346-348.
- Burt, William H. 1933. On the breeding habits of pocket gophers. *Murrelet*, 1933 (May). 1 p.
- Chamberlain, Roy W. 1943. Four new species of Collembola. *Great Basin Naturalist*, 4: 39-48.
- Cook, J. B. 1939. Pocket gophers spread Canada thistle. *Calif. Dept. Agr. Bull.*, 28: 142-143.
- Criddle, Stuart. 1930. The prairie pocket gopher, *Thomomys talpoides rufescens*. *Jour. Mamm.*, 11: 265-280.
- Crouch, W. E. 1942. Pocket gopher control. U. S. Fish and Wildlife Service, Conservation Bull., 23: 1-20.
- Dalquest, Walter W., and Victor B. Scheffer. 1942. The origin of the mima mounds of western Washington. *Jour. Geol.*, 50: 68-84.
- . 1944. Distribution and variation in pocket gophers, *Thomomys talpoides*, in the state of Washington. *Amer. Nat.*, 78: 308-333.
- Davis, W. B. 1938. Relation of size of pocket gophers to soil and altitude. *Jour. Mamm.*, 19: 338-342.
- . 1939. The recent mammals of Idaho. Caldwell, Idaho: Caxton Printers, Ltd. 400 pp.
- Davis, W. B., R. R. Ramsey, and J. M. Arendale, Jr. 1938. Distribution of pocket gophers (*Geomys breviceps*) in relation to soils. *Jour. Mamm.*, 19: 412-418.
- Dice, Lee R. 1939. *Thomomys* the engineer—friend or foe? *Amer. Forests*, 1939 (Oct.). 1 p.
- Dixon, Joseph. 1922. Rodents and reclamation in the Imperial Valley. *Jour. Mamm.*, 3: 136-146.
- . 1929. The breeding season of the pocket gopher in California. *Jour. Mamm.*, 10: 327-328.
- Ellison, Lincoln. 1946. The pocket gopher in relation to soil erosion on mountain range. *Ecology*, 27: 101-114.
- English, Pennoyer F. 1932. Some habits of the pocket gopher, *Geomys breviceps breviceps*. *Jour. Mamm.*, 13: 126-132.
- Evans, F. C., and J. T. Emlen, Jr. 1947. Ecological notes on the prey selected by a barn owl. *Condor*, 49: 3-9.

- Fitch, Henry S., and Jay R. Bentley.** 1949. Use of California annual-plant forage by range rodents. *Ecology*, **30**: 306-321.
- Gabrielson, Ira N.** 1938. *Thomomys* the engineer. *Amer. Forests*, 1938 (Oct.).
- Goldman, E. A.** 1947. The pocket gophers (genus *Thomomys*) of Arizona. U. S. Fish and Wildlife Service, N. Amer. Fauna, No. 59. 39 pp.
- Grinnell, Joseph.** 1923. The burrowing rodents of California as agents in soil formation. *Jour. Mamm.*, **4**: 137-149.
- . 1926. Geography and evolution in the pocket gopher. *Univ. Calif. Chron.*, 1926: 247-262. Reprinted in *Smith. Inst. Ann. Report*, 1926: 343-355, 1927.
- Grinnell, Joseph, and Tracy I. Storer.** 1924. Animal life in the Yosemite. xviii + 752 pp. Berkeley: Univ. Calif. Press.
- Hall, E. Raymond.** 1946. Mammals of Nevada. xi + 710 pp. Berkeley: Univ. Calif. Press.
- Hill, J. E.** 1934. External characters of newborn pocket gophers. *Jour. Mamm.*, **15**: 244-245.
- . 1937. Morphology of the pocket gopher mammalian genus *Thomomys*. *Univ. Calif. Publ. Zool.*, **42**: 81-171.
- Hisaw, F. L.** 1925. The influence of the ovary on the resorption of the pubic bones of the pocket gopher, *Geomys bursarius* (Shaw). *Jour. Exp. Zool.*, **42**: 411-433.
- Hisaw, F. L., and H. K. Gloyd.** 1926. The bullsnake as a natural enemy of injurious rodents. *Jour. Mamm.*, **7**: 200-205.
- Holliger, C. D.** 1916. Anatomical adaptations in the thoracic limb of the California pocket gopher and other rodents. *Univ. Calif. Publ. Zool.*, **13**: 447-494.
- Horn, E. E.** 1923. Some notes concerning the breeding habits of *Thomomys townsendi*, observed near Vale, Malheur County, Oregon, during the spring of 1921. *Jour. Mamm.*, **4**: 37-39.
- Howard, Walter E.** 1951. Relation between low temperature and available food to survival of small rodents. Accepted for publication in *Jour. Mamm.*, **32**.
- . MS. A live trap for pocket gophers. Accepted for publication in *Jour. Mamm.*
- Howell, A. B.** 1922. Surface wanderings of fossorial mammals. *Jour. Mamm.*, **3**: 19-22.
- Hubbell, T. H., and C. C. Goff.** 1939. Florida pocket gopher burrows and their arthropod inhabitants. *Florida Acad. Sci.*, **4**: 127-166.
- Imler, R. H.** 1945. Bullsnakes and their control on a Nebraska wildlife refuge. *Jour. Wildlife Management*, **9**: 265-273.
- Ingles, Lloyd G.** 1949a. Field observations on the growth of young mountain pocket gophers. *Murrelet*, **30**: 35-36.
- . 1949b. Ground water and snow as factors affecting the seasonal distribution of pocket gophers, *Thomomys monticola*. *Jour. Mamm.*, **30**: 343-350.
- . 1949c. An improved live trap for pocket gophers. *Murrelet*, **30**: 55-56.
- Ingles, L. G., R. Clothier, and L. A. Crawford.** 1949. Methods of estimating pocket gopher populations. *Jour. Wildlife Management*, **13**: 311-312.
- Johnson, C. E.** 1926. Notes on a pocket gopher in captivity. *Jour. Mamm.*, **7**: 35-37.
- Kelly, A. O.** 1948. The mima mounds. *Scientific Monthly*, **66**: 174-175.
- Lantz, D. E.** 1918. Rodent pests of the farm. U.S.D.A., *Farmers' Bull.*, No. 932. 23 pp.
- Larrison, Earl J.** 1942. Pocket gophers and ecological succession in the Wenas region of Washington. *Murrelet*, **23**: 34-41.
- Marshall, W. H.** 1941. *Thomomys* as burrowers in the snow. *Jour. Mamm.*, **22**: 196-197.
- Merriam, C. H.** 1895. Monographic revision of the pocket gophers, family Geomyidae (exclusive of the species of *Thomomys*). U.S.D.A., N. Amer. Fauna, No. 8. 258 pp.
- Miller, Milton A.** 1946. Reproductive rates and cycles in the pocket gopher. *Jour. Mamm.*, **27**: 335-358.
- . 1948. Seasonal trends in burrowing of pocket gophers (*Thomomys*). *Jour. Mamm.*, **29**: 38-44.
- Miller, Milton A., and Walter E. Howard.** 1951. The size of bait for pocket gopher control. *Jour. Wildlife Management*, **15**: in press.
- Mohr, C. O., and W. P. Mohr.** 1936. Abundance and digging rate of pocket gophers, *Geomys bursarius*. *Ecology*, **17**: 325-327.
- Price, W. Armstrong.** 1949. Pocket gophers as architects of mima (pimple) mounds of the western United States. *Texas Jour. Sci.*, **1**: 1-17.
- Sagal, Bernice E.** 1942. Natural history of the pocket gopher, *Thomomys bottae*, of Alameda County, California. Thesis (M.A.), Univ. Calif. Library, Berkeley, 92 pp.
- Scheffer, T. H.** 1931. Habits and economic status of the pocket gophers. U.S.D.A., *Tech. Bull.*, **224**: 1-26.
- . 1934. Hints on live trapping. *Jour. Mamm.*, **15**: 197-202.
- . 1938. Breeding records of Pacific Coast pocket gophers. *Jour. Mamm.*, **19**: 220-224.
- . 1940. Excavation of a runway of the pocket gopher (*Geomys bursarius*). *Trans. Kansas Acad. Sci.*, **43**: 473-478.
- . 1945. Burrow associations of small mammals. *Murrelet*, **26**: 24-26.
- . 1948. Mound construction of the pocket gopher. *Murrelet*, **29**: 9-10.

- Scheffer, Victor B. 1947. The mystery of the Mima mounds. *Scientific Monthly*, 65: 283-294.
- Sherman, H. B. 1941. A box trap for the capture of live *Geomys*. *Jour. Mamm.*, 22: 182-184.
- Sherman, H. B., and B. A. Barrington. 1941. A pocket gopher cage. *Jour. Mamm.*, 22: 91-93.
- Smith, C. F. 1940. Weights of pocket gophers. *Jour. Mamm.*, 21: 220.
- Stallings, J. H. 1948. The mima mounds. *Scientific Monthly*, 66: 269-270.
- Storer, Tracy I. 1949. Control of field rodents in California. *Univ. Calif. Agr. Ext. Serv. Circ.*, 138: 1-50.
- Storer, Tracy I., and Paul W. Gregory. 1934. Color aberrations in the pocket gopher and their probable genetic explanation. *Jour. Mamm.*, 15: 300-312.
- Taylor, Walter P. 1935. Some animal relations to soils. *Ecology*, 16: 127-136.
- . 1948. Outlines for study of mammalian ecology and life histories. *U. S. Fish and Wildlife Service, Wildlife Leaflet*, 304: 1-26.
- Tryon, C. A., Jr. 1943. The great gray owl as a predator on pocket gophers. *Wilson Bull.*, 55: 130-131.
- . 1947. The biology of the pocket gopher, *Thomomys talpoides* in Montana. *Mont. St. Coll. Agr. Exp. Sta., Tech. Bull.*, 448: 1-30.
- Villa-R, Bernardo, and E. Raymond Hall. 1947. Subspeciation in pocket gophers of Kansas. *Univ. Kansas Mus. Nat. Hist.*, 1: 217-236.
- Wade, Otis. 1927. Food habits of a pocket gopher (*Geomys lutescens*). *Jour. Mamm.*, 8: 310-311.
- Warren, E. R. 1937. Notes on pocket gophers. *Jour. Mamm.*, 18: 473-477.
- Wight, H. M. 1918. Life history and control of the pocket gopher in the Willamette Valley. *Oreg. Agr. Exp. Sta. Bull.*, 153: 1-55.
- . 1930. Breeding habits and economic relations of The Dalles pocket gopher. *Jour. Mamm.*, 11: 40-48.
- Wood, John E. 1949. Reproductive pattern of the pocket gopher (*Geomys brevicauda brazensis*). *Jour. Mamm.*, 30: 36-44.
- WALTER E. HOWARD
- DIVISION OF ZOOLOGY,
UNIVERSITY OF CALIFORNIA,
DAVIS, CALIFORNIA
- LLOYD G. INGLES
- BIOLOGY DEPARTMENT,
FRESNO STATE COLLEGE,
FRESNO, CALIFORNIA

GEORGE WASHINGTON, SURVEYOR AND ECOLOGICAL OBSERVER¹

One of the best pictures of the colonial forests of the eastern United States is provided by the surveying notes and other writings of George Washington. His youthful career as a surveyor is well known. Little attention has apparently been paid, however, to the valuable ecological information recorded in the course of his surveying and other exploratory travels.

The fame of Washington, coupled with his own meticulous habits, has resulted in the preservation of much of his writing. Transcripts of his diaries, journals, and letters have been published and are easily accessible. Douglas Southall Freeman in his brilliant biography of young Washington (1948) has recently called attention to Washington's love of trees and knowledge of tree species. Following this lead, the present author has examined the transcripts of Washington's writings for the purpose of bringing together his notes concerning trees and the original forests of the central Appalachians.

There is little of interest to the forester or ecologist in Washington's accounts of his many military and political travels. His surveying

notes from 1748 to 1752, however, provide much information on the forest trees of the upper Shenandoah Valley in Virginia and adjacent areas to the west in what is now West Virginia. Later journals are of some interest in describing the Dismal Swamp in southeastern Virginia and northeastern North Carolina, and the forests along the upper Ohio River.

SURVEYING CAREER

As a younger son of a not particularly affluent family, George Washington was faced with the problem of earning a living and building up a fortune within the limits imposed by his status as a gentleman. Land was the principal form of wealth in colonial Virginia. It was to be had almost for the taking along the frontiers of settlement, and the surveyor along these frontiers was in the ideal position to pick and choose. It was altogether natural, therefore, that young George would choose surveying, not as a profession, but as a means of acquiring land and eventually wealth. During the summer of 1747, when he was 15 years old, he began to run practice surveys with his father's compass in the neighborhood of the family farm where he was staying.

In March, 1748, George arranged through

¹ University of Minnesota Agricultural Experiment Station Misc. Jour. Series Article No. 740.

his eldest brother, Laurence Washington, to join George William Fairfax on a surveying expedition into the upper Shenandoah Valley in the vicinity of the present city of Winchester. His status was not that of a surveyor. Rather, he was travelling companion to young Fairfax who represented his father, the agent of the proprietor charged with dispensing the lands for settlement. More than that, George was a student of the surveyor, James Genn. By working with the surveyor day after day, keeping notes and doing odd jobs, he acquired the experience necessary for him to qualify as a surveyor himself. His journal of the trip includes a sample survey dated March 15, 1748, and entitled: "The Mannor how to Draw up a Return when Survey'd for His Lordship or any of ye Family." By March 31, he had progressed to the point where he was allowed to survey a lot by himself, and by the end of the month's trip, he was reasonably well qualified to be a county surveyor.

The County of Culpepper was established in 1749 and on July 20th of that year Washington presented at the County Courthouse his appointment by the President of William and Mary College as County Surveyor. For the next three years, Washington was active as a surveyor, doing most of his work in connection with the Fairfax proprietorship of the "northern neck of Virginia" in the upper Shenandoah Valley, the valley of the Cacapon, and that of the South Branch of the Potomac River. From September 28, 1751 to January, 1752, Washington accompanied his brother Laurence to Barbados in the West Indies and of course did no surveying during that time. On November 6, 1752, Washington was appointed Adjutant in the provincial military forces and this entrance into his military career terminated the surveying phase of his life. Although he did an occasional survey in later years, he did so only in connection with his own land interests.

SURVEYING TECHNIQUE

The job of the frontier surveyor was to lay out land for settlement as quickly and as inexpensively as possible. The surveying techniques of Washington were therefore of the rough and ready sort. He used a staff compass and chain. Magnetic bearings were recorded to the nearest degree and distances were measured to the nearest rod (termed "pole" by Washington). No corner stakes were set. Rather, a convenient tree was chosen as a corner, blazed, and inscribed. It is this practice of the frontier surveyor of tying-in to trees rather than stakes that provides the information concerning the forests of the time. A sample survey chosen at random from Washington's notes illustrates the type of survey and the nature of the information supplied:

April 24th 1750

Plat drawn

Then Surveyed for Thomas Wiggans a certain Tract of Waste Land Situate in Frederick County & on Potomack River about $\frac{1}{2}$ Mile above ye Mouth of great Cacapehon & bounded as followeth beg: at a white Oak a white Hickory & white Wood Tree just on ye Mouth of Wiggan's Run & opposite to a nob of ye Mountains in Maryland & run thence S° 25 W° Two hund^a & twenty Eight Poles to a white hickory an Elm & Mulberry about 30 Pole from Cacapehon thence N° 75 W° One hund^a & forty Poles to a Chesnut Oak & white Oak thence N° 25 E° Two hund^a & Sixty Poles to a white Oak red Oak & Iron Wood on ye Riverside thence down ye several Meanders thereof S° 67 $\frac{1}{2}$ E° 37 Po S° 58 $\frac{1}{2}$ E° 74 Po S° 55 E° to ye beg Con^a 210 Acres—

John Lonem

Isaac Dawson

William Wiggans

Most of Washington's surveying notes that have survived to the present day have been transcribed by Toner (1892). It is upon these that the present study is based. Fitzpatrick (1925) lists additional surveys but transcripts of these were not available to the writer.

TREES CITED

There seems to be no reasonable doubt that Washington knew the trees of the middle Appalachian regions. His reputation as a surveyor would naturally depend in part upon the accuracy of his description of corners, and this in turn depended upon the correct naming of the corner trees. Furthermore, there is a wealth of internal evidence in the surveying notes confirming this knowledge. For example, he was very precise in his identification. He named separately seven oak species, including such a relatively uncommon and confusing species as swamp white oak. He readily distinguished the two *Juglans* from each other as he did also between the two maples. In all, he listed some thirty-five different tree species, all of which are known to occur in the area and on the sites and in the associations where he placed them.

The descriptive phrases are particularly convincing as to Washington's knowledge of trees. How very typical are the descriptions "three Lynn (basswood) Trees growing from one stump," "a Black Walnut in a Poysoned Field by a Limestone Rock," and "2 Sycamores & a White Wood (yellow poplar) tree Standing in ye Fork." Certainly, Washington was a qualified observer of the forest.

Most of the species are given names still common today or at least readily identifiable. The appropriate scientific names for each are given in Table I. In a few cases, some additional comment may be made.

Spanish oak referred to by Washington could be either pin oak (*Quercus palustris*), or scarlet

oak (*Quercus coccinea*). Washington's best description referring to this species in the Cacapon Valley is: "Beginning at a Pine a Spruce Pine and Spanish Oak by the side of some Large Rocks on the East Side the River."

Washington wisely avoided naming the individual hickories except for white hickory, which is probably the mockernut hickory (*Carya tomentosa*). Note the description for the junction of the Cacapon and Potomac Rivers: "at

TABLE I. Trees cited in Washington's survey notes

Name cited	Scientific name**	Number of citations*				
		Eastern Virginia	Shenandoah	Cacapon	South Branch	Total
White oak	<i>Quercus alba</i>	20	110	221	35	386
Red oak	<i>Q. rubra</i>	7	125	37	19	188
Chesnut oak	<i>Q. prinus</i>	—	—	34	17	51
Black oak	<i>Q. velutina</i>	1	10	26	1	38
Spanish oak	<i>Q. palustris</i> (?)	2	2	17	9	30
Swamp white oak	<i>Q. bicolor</i>	—	—	4	—	4
Box oak	<i>Q. stellata</i>	—	—	—	1	1
Hickory	<i>Carya</i> sp.	3	86	44	9	142
White hickory	<i>C. tomentosa</i> (?)	—	—	3	—	3
Locust	<i>Robinia Pseudo-Acacia</i>	—	32	—	4	36
Black walnut	<i>Juglans nigra</i>	2	6	4	3	15
White walnut	<i>J. cinerea</i>	—	—	6	1	7
Maple	<i>Acer rubrum</i>	1	—	14	—	15
Sugar	<i>A. saccharum</i>	—	—	3	—	3
Burch	<i>Betula nigra</i> (?)	—	—	2	—	2
Mountain burch	<i>B. lenta</i> (?)	—	—	14	—	14
Sycamore	<i>Platanus occidentalis</i>	—	8	2	5	15
Chesnut	<i>Castanea dentata</i>	3	—	11	—	14
Gum	<i>Nyssa sylvatica</i> (?)	—	—	9	—	9
Black gum	<i>Nyssa sylvatica</i>	3	—	—	—	3
Sweet gum	<i>Liquidambar Styraciflua</i>	1	—	—	—	1
Lynn	<i>Tilia americana</i>	—	—	12	—	12
Ash	<i>Fraxinus</i> sp.	—	1	3	5	9
Poplar	<i>Populus</i> sp.	—	—	4	2	6
Whitewood	<i>Liriodendron Tulipifera</i>	—	—	2	2	4
Elm	<i>Ulmus americana</i> (?)	—	—	3	—	3
Dogwood	<i>Cornus florida</i>	1	—	1	—	2
Mulberry	<i>Morus rubra</i>	1	—	1	—	2
Red Bud	<i>Cercis canadensis</i>	—	—	—	2	2
Sassafras	<i>Sassafras albidum</i>	1	—	—	—	1
Iron Wood	<i>Carpinus caroliniana</i> (?)	—	—	1	—	1
Wild cherry	<i>Prunus</i> sp.	—	—	1	—	1
Pine	<i>Pinus echinata</i> or <i>P. virginiana</i>	—	—	107	25	132
White pine	<i>Pinus Strobus</i>	—	—	5	—	5
Pitch pine	<i>P. rigida</i>	—	—	1	—	1
Spruce pine	<i>Tsuga canadensis</i>	—	—	2	—	2
Totals		46	380	594	140	1,160

* Includes duplication where lines are common to two surveys.

** Gray's Manual, 8th Edition, 1950.

a white Oak a white Hickory & white Wood Tree just on ye Mouth of Wiggans Run & opposite to a nob of ye Mountains in Maryland & run thence S 25 W 228 poles to a white hickory an Elm & Mulberry about 30 Pole from Cacapehon.

The word "Maple" refers to red maple, and "Sugar" to the sugar maple. Washington refers to both in the same phrase: "at a Maple & Sugar at ye Mouth of ye Creek."

By "Burch," it is presumed that Washington referred to the red or river birch, since he places this by the riverside ("down the River to 2 Burches"), and distinguishes it from the "Mountain burch," probably the black birch of today.

In eastern Virginia, Washington early distinguished between the black and sweet gum. In the valley of Cacapon, though, he wrote only of gum. Since there is little sweet gum in this area today, and since Washington was such a precise observer, it may be assumed that he meant specifically black gum.

The poplar is very likely cottonwood. In one place, Washington writes of "a poplar standing in ye Fork."

Finally, Washington's pine may be either the shortleaf or the Virginia scrub pine. Both species are found in eastern West Virginia. It should be possible by careful field examination, however, to determine what pines are growing today in the immediate vicinity of Washington's surveys.

Table I presents the tree count by species and major geographical areas obtained from the Toner transcript of Washington's survey notes. It includes duplication resulting from the fact that the same tree was frequently used for a corner in more than one survey. The value of such a tally obtained from surveying notes has already been discussed by others (for instance by Lutz 1930, and Kenoyer 1934). In particular, it should be remembered that surveyors normally tend to choose the larger and the longer-lived trees for their corners, and the tally should be interpreted accordingly. Nevertheless, the nature of the colonial forests is clearly presented.

The sample from eastern Virginia is small, but is still sufficient to show that the oak forest there in 1747 had basically the same composition that it has today after two hundred years, with white oak as the dominant species.

Many more citations refer to the three river valleys in the east-central Appalachians. Here again, the oaks predominated. White oak, red oak and hickory were the characteristic species with considerable pine growing on the hills and mountain sides in the Cacapon and South Branch areas.

The notes indicate where the various trees grew in the colonial forest. As would be expected, the various sites were occupied by the same species as they are today.

On the hills and mountain sides above the Cacapon and South Branch rivers, pines, hickories, chestnut oak and other oaks were the characteristic species. The implication frequently is that the trees were generally small and not overly valuable. This is especially true for hickory. Typical descriptions are of "a Pine & two hickory bushes on the Top of a clear hill," "two Chesnut Oaks and a red Oak in amongst very steep pine Hills," "2 Chesnut Oaks & a black in Piney Ground," and "two Chesnuts and one Chesnut Oak near the side of some Large hanging Rocks on the side of a Mountain."

On the bottom near the rivers, many species are listed. Walnuts, sugar maple, ash, elm, and hickory are among those identified with this site. Typical citations include: "a red Oak Walnut & Locust in a rich spot of ground," "2 Red Bud Trees & a Black Walnut on ye West side ye Fork," and "ash, black Walnut and White Walnut."

In the Shenandoah Valley, which was already being settled when Washington was surveying there, there are many mentions of open or barren ground. Small hickories and locusts, the latter commonly occurring in groups, frequently are mentioned on these areas. We have "a Dead hickory & live red Oak & white oak Saplings in ye Barains," "2 small Locust & one Hick^y in a clear spot," "to an old black stump in ye Barrens," and "a small locust and red oak in rich Barons."

All in all, the picture of the colonial forests of the central Appalachians as reconstructed from Washington's notes is a very believable one, and one that shows relatively little change in the forest of this area over the last two hundred years.

LATER TRAVELS

After his surveying days, Washington's notes on trees become much less detailed. Here and there, however, information of ecological value is provided, especially with regard to the Dismal Swamp and the Ohio Valley.

During periods that Washington was at Williamsburg with time on his hands, he interested himself in a project to drain the great Dismal Swamp, lying to the south of the James River athwart the Virginia-North Carolina boundary. He visited there several times, but he writes more of the problem of drainage than of the vegetation. He does describe the vegetation, however, under date of October 15th, 1763, referring to what was apparently his first journey into the swamp from May 25th to 28th of that year. His diary records (Fitzpatrick 1925):

"Between Cypress Swamp and the last mentioned one (i.e., Mossey Swamp) we went on horse back not less than $\frac{1}{2}$ mile into the great Swamp without any sort of difficulty, the horse

not sinking over the fetlocks. The first quarter abounding in Pine and Galebury bushes, the Soil being much intermixed with Sand but afterwards it grew blacker and richer with many young Reed and few pines, and this it may be observed here is the nature of the Swamp in general."

The main interests of Washington, however, remained in the west. In October, 1770, he made a trip down the Ohio as far as the mouth of the Kanawha River for the purpose of picking out lands to be given as a bonus to veterans of the French and Indian wars, and incidentally for choosing which of these lands he wanted for himself as a top colonial commander in these wars. Several of his passages may be quoted as giving an excellent picture of this then undeveloped country.

On October 13th, he travelled across Laurel Hill in western Pennsylvania along approximately the present route of U. S. Route 40 down to the site of present city of Uniontown.

"The Lands we travelld over to day till we had crossed the Laurel Hill (except in small spots) was very mountainous and indifferent, but when we came down the Hill to the Plantation of Mr. Thos. Gist, the Ld. appeared charming; that which lay level being as rich and black as any thing could possibly be; the more Hilly kind, tho of a different complexion must be good, as well from the Crops it produces, as from the beautiful white Oaks that grows thereon, the white Oak in general. indicates poor Land, yet this does not appear to be of that cold kind."

Two days later, Washington travelled west across the Monongahela River to look over some lands which an agent had claimed for him on Millers Run, a branch of Shurtees Creek, between the present cities of Washington and Pittsburgh, Pennsylvania.

"The Lands which I passed over to day were generally Hilly, and the growth chiefly white Oak, but very good notwithstanding; and what is extraordinary, and contrary to the property of all other Lands I ever saw before, the Hills are the richest Land; the Soil upon the Sides and Summits of them, being as black as Coal and the Growth, Walnut, Cherry, Spice Bushes, etca.; the flats are not so rich; and a good deal more mixed with Stone."

Leaving the last settlement and proceeding to the Ohio River, Washington and his party canoed downstream to the Kanawha River which he ascended a few miles and reported on November 2nd that:

"This Bottom next the Water (in most places) is very rich; as you approach to the Hills you come (in many) to a thin white Oak Land, and poor; the Hills as far as we could judge were from a half a Mile to a Mile from

the River; poor and steep in the parts we see, with Pine growing on them; whether they are generally so, or not, we cannot tell but I fear they are."

This seemed the best Virginia land available for soldier's bonus grants, and the next day they started back, marking out the land roughly:

"We set of down the River on our return homewards, and Incampd at the Mouth; at the Beginning of the Bottom above the junction of the rivers, and at the Mouth of a branch on the East side, I markd two maples, an Elm, and Hoopwood Tree as Cornr. of the Soldiers Ld. (if we can get it) intending to take all the bottom from hence to the Rapids in the Great Bent into one Survey. I also markd at the Mouth of another Gut lower down on the West side (at the lower end of the long bottom) an Ash and hoopwood for the Beginning of another of the Soldiers Survey, to extend up so as to include all the Bottom (in a body) on the West side."

On November 4th, while ascending the Ohio River en route home, Washington took time off to measure some very large sycamores. The largest with a diameter three feet from the ground of 14 feet, 3 inches, was probably somewhat larger than the present-day record which is growing near Beverly and Waterford, Ohio, and has a diameter at breast height (4 feet, 6 inches from the ground) of 13 feet, 6 inches (American Forestry Assoc. 1945).

"at the end of the Bottom from the Kanawha, just as we came to the Hills, we met with a Sycamore abt. 60 yards from the River of a most extraordinary size, it measuring (3 feet from the Gd.) 45 feet round, lacking two Inches, and not 50 yards from it was another 31.4 round (3 feet from the Gd. also)."

On November 17th, while near Buffalo Creek in present-day Jefferson County, Ohio, Washington wrote a general description of the forests of the Ohio Valley.

"The Bottom Land differs a good deal in quality, that highest up the River in general is richest; tho the Bottoms are neither so wide or long, as those below. Walnut, H. Locust Cherry, and some other Woods, that grow Snarly, and neither Tall nor large, but covered with Grape Vines (with the Fruit of which this Country at this Instant abounds) are the growth of the richest Bottoms; but on the other hand these Bottoms appear to me to be the lowest and most subject to Floods. Sugar tree and Ash, mixd with Walnut, etca. compose the growth of the next richest low grounds, and Beach, Poplar, Oaks, etca. the last. The soil of this is also good but inferior to either of the other kinds, and beach Bottoms are excepted against on acct. of the difficulty of clearing the, there Roots spreading over a large Surface of Ground and being hard to kill."

Other citations of interest may be made from the notes of Washington's 1770 trip and from later trips such as his trip to western Pennsylvania in 1784 (Hulbert 1905). Those given above, however, are among the best and should suffice to justify the inclusion of George Washington with those colonial travellers whose shrewd and accurate observations give us much information concerning the colonial forests of the United States.

LITERATURE CITED

- American Forestry Association.** 1945. Report on American big trees. *American Forests* 51: 30-36.
- Fernald, M. L.** 1950. Gray's manual of botany. Eighth (Centennial) edition. American Book Company. New York.
- Fitzpatrick, John C.,** Editor. 1925. The diaries of George Washington. 1748-1799. Houghton Mifflin Company. New York. Vol. 1. 1748-1770.
- Freeman, Douglas Southall.** 1948. George Washington. A biography. Vol. 1 and 2. Young Washington. Charles Scribner's Sons. New York.
- Hulbert, Archer Butler.** 1905. Washington and the west. The Century Co. New York.
- Kenoyer, L. A.** 1934. Forest distribution in southwestern Michigan as interpreted from the original land survey (1826-32). *Michigan Acad. Sci., Arts and Letters Papers* 19: 107-111.
- Lutz, H. J.** 1930. Original forest composition in Northwestern Pennsylvania as indicated by early land survey notes. *Jour. Forestry* 28: 1098-1103.
- Toner, Joseph Meredith.** 1892. Journal of my journey over the mountains by George Washington, while surveying for Lord Thomas Fairfax, Baron of Cameron, in the Northern Neck of Virginia beyond the Blue Ridge, in 1747-8. Privately printed. Albany, N. Y.
- STEPHEN H. SPURR
- SCHOOL OF FORESTRY,
UNIVERSITY OF MINNESOTA,
ST. PAUL, MINNESOTA

WINTER INACTIVITY OF SOME CAPTIVE CHIPMUNKS (*TAMIAS S. STRIATUS*) AT CHAPEL HILL, NORTH CAROLINA

INTRODUCTION

Although truly dormant chipmunks occasionally have been discovered under natural conditions (Howell 1929), and although torpidity, accompanied by greatly lowered body temperatures, has been induced in the laboratory (Woodward and Condren 1945), so that chipmunks must be counted among the true hibernators, it has been noted in northern states that this small mammal often is active above ground during warm weather in the winter (Hamilton 1939, 1943). It might be supposed, therefore, that in lower latitudes, where the whole winter is characteristically mild, chipmunks either would not hibernate at all or would hibernate only during the relatively short and infrequent "cold" spells. This supposition is implicit in a discussion of chipmunk habits in Virginia (Bailey 1946). It also has been said that chipmunks in North Carolina "probably hibernate to some extent in the mountains, but not in the Piedmont section" (Brimley 1945).¹

The following observations, made at Chapel Hill, North Carolina, in the lower section of the Carolina Piedmont, do not include any direct observations of dormancy, but the indirect evidence for true hibernation is very strong. They show that in this region some individual chipmunks fail to appear above ground during extensive periods of weather of such warmth as must seldom be attained in winter in the north-

ern woods, and that they remain continuously underground for periods of time that approach or exceed in their duration those recorded for northern climates. They also show, perhaps not surprisingly, considerable variation between individuals during the same season, as well as marked variation in the same individual in successive seasons. Unfortunately, the observations were not made under a planned study of chipmunk hibernation, but were simply collected, in part casually, on some individuals I was trying to mate; as a result, certain rather pertinent data were not obtained.

METHODS

The chipmunks were held in an outdoor pen approximately 10 feet long by 8 feet wide. In constructing this pen a pit was dug in the ground, and lined with brick, the bricks of the floor set in sand, rather than mortar, to provide drainage. The pit was then refilled with 20 inches of dirt and rock, to a level approximately even with the surrounding ground. Over it a cage 2 feet high was constructed, made of $\frac{1}{4}$ "-mesh hardware cloth on a wooden frame. Both cage and pit were divided into 4 sections, thus giving 4 pens each about 5 feet by 4 feet in area. Two males and two females were kept in these outdoor enclosures, one chipmunk in each pen. A small opening between adjacent pairs allowed either member of the pair to enter the pen of the other;

but these openings were closed throughout the winter months, when each chipmunk was isolated in a separate pen.

Chipmunks have occasionally disappeared from these pens, presumably having died underground, but this has never occurred during the winter months. Breeding success has not been high, only 2 litters resulting from 6 possible matings, but irregularity of emergence of the animals in spring is, very likely, one of the factors responsible for this. In general, the chipmunks appear to be normal and healthy in these confined, but otherwise natural, quarters.

The chipmunks were fed almost exclusively on sunflower seeds and apple; but acorns were frequently given during the fall, less frequently in the spring. Apples provided an apparently entirely adequate source of water. Usually a small handful of sunflower seeds was given at a time, together with a slice of apple. They were fed daily, the seeds scattered on the ground of the pen. And here is my only test for "hibernation"—perhaps more precisely, for "absence of above-ground activity." All during the late spring, summer, and early fall, any food so given disappeared within less than an hour. I have often stood quietly by, after throwing feed into the pens, and watched the chipmunks pop up from their burrows within a few minutes and scurry about, almost frantically, it would seem, stuffing their cheek pouches with seed, darting then back underground, only to reappear in a moment and resume their foraging, not stopping until all was stored away below ground. The apple was eaten above ground, and a small number of seeds, but the storing activity went on almost unceasingly, as long as food remained on the surface. There was nothing seasonal about this behavior, it occurred at all times of the year. With individuals active in winter, however, some hours might on occasion elapse between the offering of the food and the emergence of the animal. But once emerged the gleaning immediately began, and went quickly to its completion. As an example, once, in the late fall, I strewed enough acorns in one pen to fill a one-pound coffee-can; the single chipmunk occupant carried every one of those acorns underground in less than 20 minutes! When, therefore, a day or two or more, a week or months went by with seeds lying undisturbed on the ground, I could assume only that the occupant of the pen either was dead, or was hibernating, or at most was confining its activity, if any, strictly to its den or burrow. It should be noted that, for true hibernators, the one and only criterion for establishing the period of hibernation *in nature* is the one used in this study, namely the absence of activity above ground. The validity of the daily test used for determining absence of activity above ground is hardly open to question by anyone who knows chipmunks. It sim-

ply is not credible that a chipmunk would emerge from his burrow and not remove a little pile of sunflower seeds lying within a foot of the burrow entrance.

RESULTS OF OBSERVATIONS

It will be noted that in 1948-1949 (Table I), although one female was more or less continuously active, 3 other chipmunks remained continuously underground for rather lengthy periods (91, more than 124, and 143 days, respectively; or from 13 to 20 weeks). The active female (No. 1) was an old adult, in her

TABLE I. *Calendar of activity for 4 chipmunks in outdoor pens, Chapel Hill, North Carolina, winter of 1948-1949. Pens observed daily from 1st week of November to 1st week of April*

Animal	Periods of complete absence of activity above ground		Succeeding interval (days) of activity above ground
	Inclusive dates	Duration (days)	
No. 1 ♀	Nov. (7)-Nov. 18	12+	20
	Dec. 9-Dec. 10	2	18
	Dec. 29-Jan. 2	5	2
	Jan. 5-Jan. 7	3	23
	Jan. 31	1	5
	Feb. 6-Feb. 7	2	25
	Mar. 5-Mar. 7	3	Cont.
No. 2 ♀	Nov. 4-Nov. 7	4	1 ^a
	Nov. 8-Mar. 26	143	2 ^b
	Mar. 29-Apr. 5	8	3 ^c
No. 3 ♂	Nov. (7)-Mar. 11	124+	3
	Mar. 15-Mar. 24	10	14
	Apr. 8- ?	(Several) ^d	—
No. 4 ♂	Nov. (7)-Nov. 19	13+	1
	Nov. 20-Dec. 3	13	1
	Dec. 4-Mar. 5	91	14 ⁻
	Mar. (19)-Apr. (11)	22+	Cont.

Parentheses indicate date not definitely determined, but known to be previous to initial date given, or later than terminal date. *Cont.*: period of activity continuous from then on.

^a: This pen was partially dug out on the afternoon of November 7, when an apparently new but empty nest was discovered; next morning food had been removed, as well as some nesting material that had been left above ground. ^b: A second female was introduced into this pen on March 11, but removed on the reappearance, 2 weeks later, of number 2 (an easily recognized, near-white individual). ^c: Number 2 again disappeared for 10-15 days during the middle of April; no exact dates. ^d: Systematic observations not made after April 12, but this individual seen regularly from about middle of May on.

TABLE II. *Calendar of activity for 4 chipmunks in outdoor pens, Chapel Hill, North Carolina, winter of 1949-1950 (including 3 of the 4 individuals on the 1948-1949 calendar). Pens observed daily from October through May*

Animal	Periods of complete absence of activity above ground		Succeeding interval (days) of activity above ground
	Inclusive dates	Duration (days)	
No. 1 ♀	Nov. 15-May 12	178	Cont.
No. 3 ♂	Dec. 5	1	7
	Dec. 13-Dec. 15	3	1
	Dec. 17-Dec. 25	9	24
	Jan. 19	1	60
	Mar. 22-May 2	42	2
	May 5-May 8	4	Cont.
No. 4 ♂	Oct. 30-Nov. 2	4	27
	Nov. 30-Dec. 1	2	13
	Dec. 10-Dec. 13	3	1
	Dec. 14-Dec. 19	6	102
	Apr. 1-Apr. 8	8	2
	Apr. 11-Apr. 15	5	Cont.
No. 5 ♀	Nov. 15-Apr. 1	137	8
	Apr. 10	1	1
	Apr. 12-Apr. 25	14	Cont.

third year and second full winter in the pen. The other female (No. 2) had been captured, fully grown, the previous spring (1948) and had been confined during the summer in an indoor cage. The two males had been born in the pen in the spring of 1948, but had spent the summer in small indoor cages. The lengthy records, thus, were made by individuals spending their first winter in the relatively confined quarters of the pen. Yet, no correlation is possible here, because in the ensuing winter (Table II), female No. 1, in her third full winter in the pen, remained continuously underground for 178 days—lacking only four days of a full half-year of inactivity! Conversely, the two males, now in their second year in the pen, remained almost continuously active, except for a 42-day disappearance of No. 3 in the spring. Female No. 5, like the two males, had never known unlimited freedom; she was born in the pen in the spring of 1948, and spent the next 17 months in a small indoor cage, being returned to the outdoor pen in the fall of 1949, where she shortly went underground, to stay 137 days.

For the record, for what it may be worth, these last 3 individuals (No. 3, No. 4, No. 5) were siblings, whose mother was No. 1. Some additional data are available for this female (No. 1) from a previous winter, her first full winter in the outdoor pen, which immediately preceded

her pregnancy resulting in the litter of which No. 3, No. 4, and No. 5 were members. These data are incomplete for the fall, and for the spring, but the records show that no food disappeared from her cage from December 27, 1947 until February 15, 1948, an interval of at least 50 days. During this period food disappeared almost daily from the pen of her mate. On February 1 there was a fairly heavy fall of snow (7 in.). Two days later the male had burrowed up to the surface, leaving a clean round hole, but since there were no tracks he obviously did not come out on the surface. Food placed at the edge of his burrow entrance was gone the next morning. Before this snow had completely disappeared, the weather remaining cold, a second snowfall, a little heavier than the first (10 in.), fell on February 9/10. This was dissipated by a warm front with very strong winds during the night of February 13/14. February 14 was mild, but drizzly; the female emerged next morning, when it was sunny and mild (predawn low of 26° F., but rising to 57° F. during the day). She again disappeared sometime between March 17 and March 27, and reappeared April 10, an interval of at least 14 days, perhaps 24 days. She had evidently meanwhile passed through her period of gestation, and gave birth to her young probably shortly after this last reappearance, since they were first observed above ground on May 14, and young chipmunks are said to spend the first 30-31 days in the nest (Hamilton 1943).

Complete weight records for all of these chipmunks would be desirable, but unfortunately the data are incomplete. The data I do have indicate a weight loss, during the long periods spent below ground, comparable to the weight losses recorded for many true hibernators (Johnson 1931). Thus, female No. 1, who weighed 98.4 grams on October 28, 1949, 2½ weeks before disappearing on her 6-months-long sojourn underground, weighed 82.1 grams on May 13, 1950, the day after her reappearance, which is a weight loss of about 16%. Female No. 5 weighed 83.6 grams on November 6, 1949, a week before her disappearance for 20 weeks; on April 3, 1950, 2 days after her reappearance, she weighed 62.3 grams, a loss in weight of about 25%.

DISCUSSION

Truly dormant chipmunks have occasionally been discovered in natural surroundings (literature reviewed in Howell 1929). That the species does have an imperfect heat-regulating mechanism, apparently a requisite for torpidity, is indicated by the experiments of Condren (Woodward and Condren 1945), who succeeded in depressing the body temperature of chipmunks to as low as 16.8° C. from a normal body temperature of about 37° C. It may be signifi-

TABLE III. *Some air temperature data for Chapel Hill, North Carolina, winter of 1948-1949. Compare with Table I*

Month	Ave. max. (T _x) ° F.	No. of days with T _x at least		Ave. min. (T _m) ° F.	No. of days with T _m not lower than		Daily Max. T.		Daily Min. T.	
		65° F.	70° F.		40° F.	45° F.	Low	High	High	Low
Nov.	67.5	21	15	45.5	20	16	47	86	68	32
Dec.	57.7	8	4	36.8	13	5	34	76	53	14
Jan.	62.4	13	8	41.2	18	12	38	79	58	24
Feb.	61.9	11	9	43.1	17	12	50	78	61	26
Mar.	66.6	17	11	39.6	14	12	46	88	64	22
Apr. 1-10	—	—	—	—	—	—	58	80	53	36

cant that Condren's published data indicate a close correlation between the degree of depression of body temperature and the degree of depression of the blood-sugar level.

Since published statements regarding mid-winter activity of chipmunks in the northern states always couple this activity with "warm weather" or "mild spells," it is of interest to consider the state of the weather in Chapel Hill during the winters of 1948-1949 and 1949-1950; in these winters some individual chipmunks apparently hibernated, or at least were not active above ground, for continuous periods which varied from 6 to more than 25 weeks, although these were quite "mild" winters even for this section of the upper South.

The summary of some air-temperature data (Tables III and IV) emphasizes the mildness of the weather throughout both periods. Although below-freezing temperatures were recorded as minima every month in both winters, sub-zero temperatures were not even approached, nor was there a single day on which the maximum was below freezing. On the other hand, average daily minimum temperatures exceeded 40° F. in January of both years, and in February, 1949. During every month in both winters, the minimum was frequently above 45° F., the maximum above 70° F. The Chapel Hill weather

data for January and February, in 1949 and 1950, may be compared to the same data for Burlington, Vermont, a locality more or less typical for northern chipmunks. The maximum temperatures averaged 30° F. higher at Chapel Hill, and the minimum temperatures were 27° F. higher. In fact, during each of these four months, the *lowest* maximum and *lowest* minimum temperatures recorded at Chapel Hill were well above the *average* for these temperatures at Burlington. No snow fell in Chapel Hill; in Burlington the snow fall averaged over 17 inches per month. The minimum temperature at Chapel Hill was never below 0° F., and at or below 32° F. on the average only 5 days per month. At Burlington, the minimum was below 0° F. an average of 7 days per month, and at or below 32° F. an average of 27.5 days per month, or practically daily.

In view of the facts that, in each winter, at least one chipmunk of the four under observation remained more or less active, and that there was little correspondence in their periods of inactivity, it would appear futile to try to correlate the individual periods of activity or inactivity with variations in the weather. However, the complete data for 1949-1950, as presented graphically in Figure 1, bring out some interesting points.

TABLE IV. *Some air temperature data for Chapel Hill, North Carolina, winter of 1949-1950. Compare with Table II and Figure 1*

Month	Ave. max. (T _x) ° F.	No. of days with T _x at least		Ave. min. (T _m) ° F.	No. of days with T _m not lower than		Daily Max. T.		Daily Min. T.	
		65° F.	70° F.		40° F.	45° F.	Low	High	High	Low
Nov.	62.3	12	5	37.5	11	5	45	75	51	25
Dec.	56.1	9	2	35.9	9	6	38	71	59	21
Jan.	64.5	14	12	42.3	18	14	38	77	59	24
Feb.	58.0	5	1	35.3	9	5	44	77	55	17
Mar.	62.9	10	7	37.0	11	8	42	85	59	21
Apr.	73.2	24	21	44.5	19	15	50	88	61	28
May 1-14	—	—	—	—	—	—	71	94	68	39

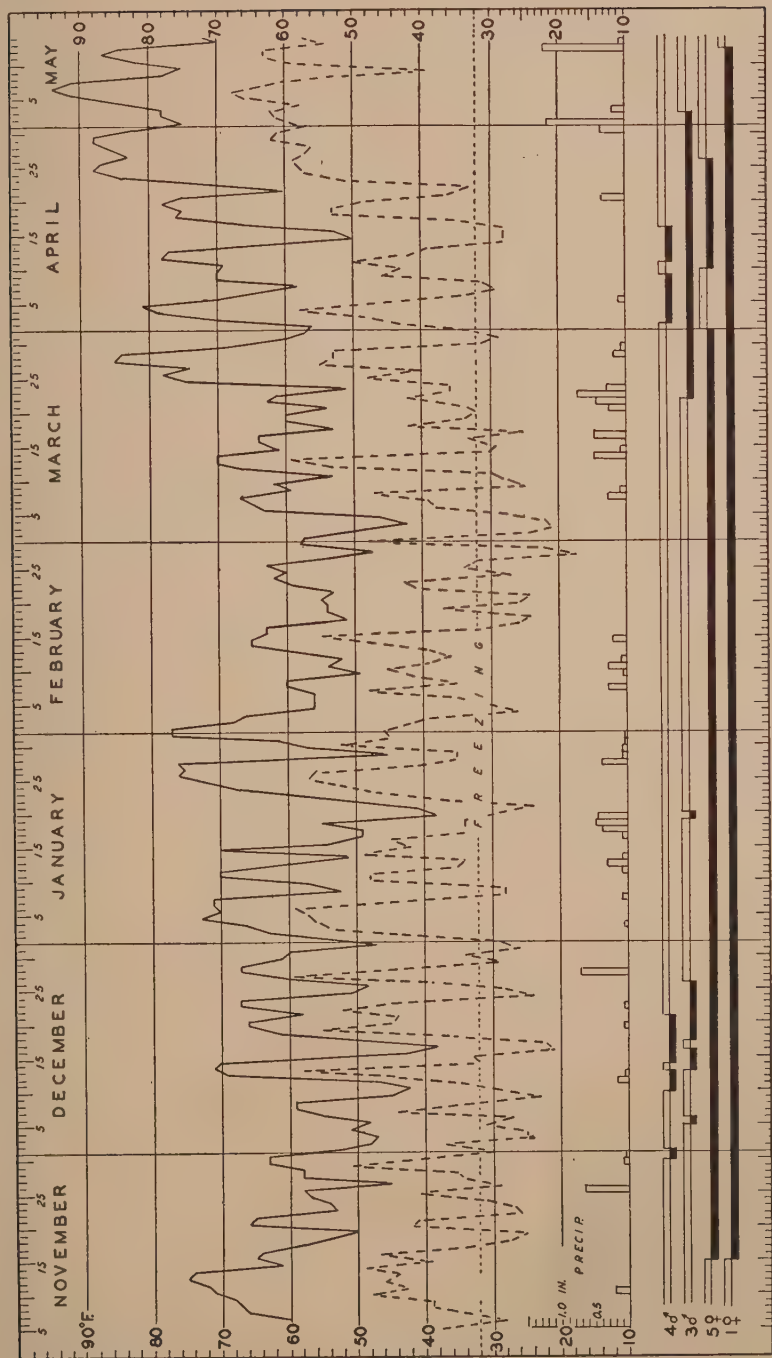


FIG. 1. Daily maximum and minimum temperature, precipitation, and chipmunk activity, Chapel Hill, North Carolina, winter of 1949-1950. Precipitation in form of rain only, no snow recorded. Chipmunk activity: open lines, daily foraging above ground; solid bars, complete absence of above-ground activity (hibernation?).

The two chipmunks that remained underground the whole winter began this period of inactivity on the same day, November 15, following a drop in the minimum temperature from 49° F. to 39°, and a drop in the maximum of the previous day from 84° F. to 61°. However, 9 days previously, a drop in the minimum temperature from 39° F. to 28° did not cause them to remain underground.

Of the two individuals which were active throughout the winter, the short periods of failure to show almost invariably began on days when the pre-dawn minimum had been below 40° F., although No. 3 began one 3-day period of inactivity following a night with minimum temperature of 58° F. Yet both these chipmunks remained active throughout a 3-month period, December 26—March 21, despite the fact there were 26 nights with below-freezing temperatures, 10 of them with temperatures 25° or less. They foraged above ground every day during this long period which included the longest continuous cold spell of the winter, February 16—March 5, when on 13 of 17 days the minimum temperature was at or below freezing.

The record for No. 3♂ is quite remarkable in that he went below ground for 6 weeks in the spring, after having been active for 3 months during the winter. He began this period of inactivity during a general temperature rise. Subsequently, while he was underground, four 3-day "cold waves" occurred at approximately 8-day intervals. During these cold waves minimum temperatures were close to or below freezing, yet during the warmer intervals maximum temperatures ranged from 70° F. to 85°, with minima above 50° F. During the last 9 of his 42 days underground, the minimum was never below 56° F. (3 times over 60°) and the maximum was never below 75° F. (on 3 days it reached 88°).

It is also noteworthy that during the last 18 days of the 6-months-long sojourn underground of No. 1♀, the average daily maximum temperature was 84° F., the average daily minimum was 59° F.

I do not know of any published study of possible geographic variation of hibernation, although the lack of such a study is rather surprising in view of the former preoccupation of students of hibernation with temperature and lack or desiccation of food sources as causal factors. Detailed comparison, in some respects, with data presented above is offered by Smith's (1931) calendar of hibernation of the chipmunk in Vermont. As a result of daily field observations from 1926 to 1928, he declares that all chipmunks in the Wells River, Vermont, area hibernate at least from October to March, the last one being seen in the woods on October 24, on the average, the first one in the spring on March 21, an interval of 21 weeks. Some individuals in the

North Carolina Piedmont (Tables I and II) cover almost this same period underground, disappearing a little later in the fall, but sometimes emerging much later in the spring. Smith mentions only a single instance of a chipmunk seen between the dates given above, hence by implication a rare event. It would not be a rare event in Chapel Hill, but it is true here that chipmunks are very infrequently seen in winter, as compared to spring, summer and fall. Smith (1931) gives one record of an individual chipmunk which apparently entered into hibernation on October 10 and did not emerge from his burrow (the mouth of which Smith had partially covered) until April 5. This lengthy interval of hibernation in Vermont is almost exactly equalled by my North Carolina female (No. 1) in 1949–1950 (November 15–May 12).

During the 3 years of Smith's spring records, the average daily maximum temperature during the week preceding his first date of emergence was only 43° F., while the average daily minimum was 23° F. Compared to the Chapel Hill temperatures given above, these figures show, as expected, that the Vermont winter and spring climate is much more rigorous. Yet some, at least, of the North Carolina chipmunks behave in their mild winter climate, with respect to "absence of above-ground activity," exactly as do their Vermont brethren under really wintry conditions.

If, as is generally assumed, hibernation is a means of evading the rigors of winter and the difficulties imposed by a diminishing and largely hidden (i.e., snow-covered) food supply, the necessary adjustments in racial physiology must have been made in our southern chipmunks at least as far back in time as the last glacial period, when our climate was more nearly like that of more northern regions today. At any rate, the very fact that chipmunks hibernate in regions of lower as well as higher latitudes, under the very different climatic conditions of northern Vermont and the Carolina Piedmont, points up the idea that the mechanism of hibernation undoubtedly is a deep-seated racial characteristic, with an evolutionary history and a genetic basis, perhaps not now as well established in individuals living in the southern parts of the species' geographic range as in the northern, but manifesting itself there nevertheless, even under mild climatic conditions and with an abundant and available food supply.

The individual variations, in the absence of any correlation with environmental temperature, suggest the existence of an inherent physiological annual cycle, in which different individuals reach critical stages at various times. The cycle thus appears to express itself independently of external stimuli, or at least at quite variable thresholds of external stimuli. What the mech-

anism of such an inherent annual cycle may be we do not know as yet. However, seasonal variation in blood-sugar concentration and also in weight of adrenal glands apparently has been demonstrated in chipmunks kept throughout the year at room temperature (Woodward and Condrin 1945). Since the maintenance of a constant blood-sugar level depends upon the adrenal cortex, and since blood-sugar is an important factor on the heat production side of the heat regulating process, seasonal variation in these factors amounts to seasonal variation in the ability adequately to compensate, with heat production, for heat loss. If heat loss should overbalance heat production, the body temperature would fall, and if this were sufficiently lowered the torpidity characteristic of hibernation would result. It has been denied by Lyman (1943) that a lowered blood-sugar level *precedes* hibernation of ground-squirrels, and claimed by him that it is therefore simply an accompaniment, not a cause, of hibernation, but it appears to me that his data, as presented, are questionable in supporting this interpretation.

SUMMARY

1. Certain chipmunks (*Tamias s. striatus*) kept in individual outdoor pens at Chapel Hill, in the North Carolina Piedmont, remained underground continuously for periods of 6, 13, 17, 19, 20 and 25 weeks during the winters 1948-49 and 1949-50. At the same time, one or more chipmunks in adjacent pens foraged above ground daily throughout the winter. Absence of activity above ground was determined by the non-disappearance of food from the surface of the ground.

2. Individual chipmunks behaved differently in the two winters, being more or less active throughout one, entirely inactive (i.e., not foraging above ground) throughout the other. For some, inactivity characterized their first winter in the pen, while others remained active throughout their first winter, but were inactive through most of the second.

3. Both winters were quite mild, even for this section of the upper South. Daily minimum temperatures averaged above 40° F. in January, 1950 and in both January and February, 1949. No snow fell in either winter. During the last

18 days of a 178-day period of inactivity for one individual, daily maximum temperatures averaged 84° F., minimum temperatures 59° F. Another chipmunk, after being active all winter, did not forage above ground for 42 days in the spring, during a time of generally rising temperature. There was little correspondence in the periods of activity or inactivity for the several individuals, and no evidence of correlation of inactivity with environmental temperature.

4. The facts are discussed in reference to some general ideas concerning hibernation. The probability of the existence of an inherent annual cycle, more or less independent of environmental conditions, is suggested.

LITERATURE CITED

- Bailey, J. W. 1946. The mammals of Virginia. xvi + 416 pp. Richmond, Va.
 Brimley, C. S. 1945. The mammals of North Carolina, No. 9. Carolina Tips, 8 (1): 3. Elon College, N. C.: Carolina Biol. Supply Co.
 Hamilton, W. J., Jr. 1939. American mammals. xii + 434 pp. New York: McGraw-Hill Co.
 —. 1943. The mammals of Eastern United States. 432 pp. Ithaca, N. Y.: Comstock Publ. Co.
 Howell, A. H. 1929. Revision of the American chipmunks (genera *Tamias* and *Eutamias*). North American Fauna, No. 52, U. S. Dept. Agric.
 Johnson, G. E. 1931. Hibernation in mammals. Quart. Rev. Biol., 6: 439-461.
 Lyman, R. A., Jr. 1943. The blood sugar concentration in active and hibernating ground squirrels. Journ. Mammal., 24: 467-474.
 Smith, W. P. 1931. Calendar of disappearance and emergence of some hibernating mammals at Wells River, Vermont. Journ. Mammal., 12: 78-79.
 Woodward, A. E., and Condrin, J. M. 1945. Physiological studies on hibernation in the chipmunk. Physiol. Zool., 18: 162-167.

WILLIAM L. ENGELS

DEPARTMENT OF ZOOLOGY,
 UNIVERSITY OF NORTH CAROLINA,
 CHAPEL HILL, NORTH CAROLINA

ECOLOGICAL OPPORTUNITIES IN VENEZUELA

"Venezuela is blessed with a most divers topographical outline. Although we are only a short distance from the equator, still we have a heterogeneous symposium of ecological zones. To the north are the low mountain ranges, sloping down to the Caribbean; to the west, high sierras with snow the year around, dropping down to the

Lake Maracaibo area with low swampland and heavy jungles; eastward the open prairie country, consisting of sandy loam, low scrub, shallow but swift rivers (in the rainy season), and swampland which is extremely dense in the Orinoco Delta; southward, more prairie country with large rivers and swamps throughout. . . .

"I am completely at your service for any aid I can give you, members of the Society, . . . in relation to study of tropical taxonomic groups. While my laboratory is set up for hematology and parasitology, I am fully equipped for a party of five for field work, and should any acquaint-

ances come to Venezuela do not hesitate to tell them to call on me for any aid I can give them."

Quotations of letter to Herbert C. Hanson, from Dr. George M. Hoyt, Edificio Las Piedras, Esq. Las piedras, Apto. 15, Caracas, Venezuela.

GEORGE M. HOYT

FEEDING HABITS OF ADULT SHAD (*ALOSA SAPIDISSIMA*) IN FRESH WATER¹

The American shad (*Alosa sapidissima*) is an anadromous fish that upon maturity enters streams along the Atlantic and Pacific coasts each spring and early summer to spawn. It has been the common belief of previous workers that the shad do not feed to any extent while in fresh water, accounting for the progressive decrease in fat content during their fresh water stay, the formation of spawning marks on the scales, and if their stay is prolonged, a possible cause of mortality. Leim (1924) summing up the opinions of early writers, as well as his own observations, states that "shad did not feed actively (in fresh water), but only took such things as came their way." Leach (1925) says that "after entering the rivers the shad takes but little, if any, food previous to spawning but after casting its eggs, it bites at flies or any small shining object, and has been known to take the artificial fly." Moss (1946) notes that "It is believed that adult shad eat but very little or not at all while in fresh water." Consequently, I was rather surprised, when adult, unspawned shad recently placed in a fresh water pond at the U. S. Fishery Laboratory, Beaufort, North Carolina (Sykes 1951) began actively to take a diet of ground fish as well as a liver-fish meal mix.

A total of seventeen adult shad (ten males, seven females) were placed in a fresh water pond about sixty feet square and with the water averaging two feet in depth. A small flow of fresh water from an artesian well nearby replenishes water lost from seepage and evaporation. On May 19, the water temperature was 24.5° C.

A small amount of food had been thrown into this pond since the introduction of the shad, April 17 to 25. On May 9, the shad were seen to congregate in the area where food was placed, apparently feeding.

Further observations on May 12 and 19 showed that: (1) within three minutes after food was tossed into the pond, all seventeen shad were in the feeding area eagerly swimming

through the settling food; (2) bits of food were seen to be taken by individual shad with no evidence of subsequent rejection; and (3) after the remaining food had settled to the bottom, the shad were seen to swim back and forth close to the bottom, stirring up mud and food alike in order to get the food before it had resettled—a most curious behavior.

On occasion, these shad have been observed to "fin" in order to take terrestrial insects that have accidentally fallen into the water, but they have not yet been observed to jump for low-flying insects as have the year-old juvenile shad in a neighboring pond. This chance capture of terrestrial insects would be too rare to form a substantial part of the diet of shad.

Although frequently behavior of fish under experimental conditions is quite different from that found in nature, there is some evidence that shad feed while in the rivers to spawn. For example, anglers do take considerable numbers of unspawned shad in the Connecticut River, in the Susquehanna, and in other Atlantic coast streams. Certainly shad must have more than a passive interest in food to take the artificial lures offered by fishermen. The fact that shad will choose individual organisms agrees somewhat with observations of the feeding habits of the closely-related alewives (Bigelow 1926).

Then there is the work on the related Caspian shad (*Caspialosa caspia*), Chajanova (1940), showing that shad feed equally intensively during the pre-spawning, spawning, and post-spawning periods, yet Zamakhaev (1940) found a rapid loss of hypodermic fat during spawning similar to that generally reported in our shad and in other anadromous fishes.

These observations do not explain the absence of food in the stomachs as reported in previous studies. We know that shad are "plankton feeders," characteristically swimming with their gill covers extended straining the water for food. Among the clupeids, Bigelow (1926, p. 101) notes the direct relationship between the fineness of the sieve formed by the gill rakers and the minimum size of the organisms that can be retained and utilized. In the sea the adult shad (i.e. over 40 cm.) feed to a large extent on mysids (Leim 1924) 10 to 30 mm. in length; in fresh water the largest plankton found in abundance are copepods which rarely exceed 5 mm.

¹ The shad investigation of the Fish and Wildlife Service, of which this experiment is a part, is being carried on to furnish information for fishery regulations to the Atlantic States Marine Fisheries Commission.

in length. It seems most likely, then, that the reason for the absence of food in the stomachs of shad in fresh water is that the available food is too small to be collected; we are certain that adult shad are both interested in food and capable of feeding during their stay in fresh water if the proper sized food were present.

SUMMARY

Contrary to previous reports of shad not feeding while in fresh water, mature shad placed in a fresh-water pond at the Fishery Laboratory, Beaufort, N. C., actively fed on ground fish and on a liver - fish meal mix. The shad, which are typically plankton feeders, took the food either as it settled through the water or by swimming back and forth close to the bottom, stirring up mud and food alike and straining out the food before it had resettled. Absence of food in stomachs of shad taken from fresh-water streams is probably attributable to the size of the fresh-water forms, since the available plankton is probably too small to be retained by the gill rakers and utilized for food.

CLINTON E. ATKINSON

U. S. FISHERY LABORATORY,
BEAUFORT, NORTH CAROLINA

LITERATURE CITED

- Bigelow, H. G. 1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish., 40 (Part II). 509 pp., 134 figs.
- Chajanova, L. A. 1940. The feeding of *Caspialosa caspia* (Eichev.). Trans. Inst. of Mar. Fish & Oceanog. USSR, 14: 211-237.
- Leach, Glen C. 1925. Artificial propagation of shad. Rep. U. S. Comm. of Fisheries, 1924: 459-486.
- Leim, A. H. 1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contr. Canadian Biology, N.S. 2 (11). 123 pp., 45 figs.
- Moss, D. P. 1946. Preliminary studies of the shad (*Alosa sapidissima*) catch in the lower Connecticut River. Trans. N. A. Wildlife Conference, 1946: 230-239.
- Sykes, J. E. 1951. The transfer of adult shad. Progressive Fish Culturist, U. S. Fish and Wildlife Service, 13 (1): 45-46.
- Zamakhaev, D. T. 1940. Spawning marks in the scales of some Caspian shads. Trans. Inst. of Mar. Fish & Oceanog. USSR, 14: 3-21.

HOXMARK ON THE INTERNATIONAL OLYMPIC GAMES AND THE INFLUENCE OF CLIMATE ON HUMAN ENERGY¹

The gist of the Olympic Games article is that achievement in the Olympic games is a measure of climatic energy. Proof is offered in a table and diagram showing a rough correlation between an artificial index of achievement in the games and the mean annual temperature of the competing country. Leaving aside all other arguments, error number one, and it is a fundamental one, occurs here. A correlation between two sets of phenomena never proves anything. Whether or not any correlation is causal, has always to be proved.

Even the physical side of the argument is inadequate. What is the meaning of a mean annual temperature for a country? How would one compute such a figure, 51.1° F., for the United States? Has anyone investigated the geographic origin of Olympic athletes from the United States? Don't the tennis players come from California, and the winter sports teams from New England? Unless one is willing to engage in such minimum inquiry, can one begin to deduce laws? "... the average law of the correlation between physical energy and thermal conditions" (Hoxmark, p. 153).

A further fundamental weakness is the lack of

understanding of cultural processes. The Olympic games stress activities characteristic of Western Society. To what extent then is it expectable that India, China and Africa (one-half of all mankind!) would compare well in a competition?

Even within western nations the data are prejudiced. The northwest European nations are the more advanced socially and economically. This has important influences on health and economic freedom to pursue sports. Even if the climates were uniform in Europe, one would expect some such ranking as Hoxmark found.

Hoxmark's article is such bad science that it hardly merits comment. But there is an awakening interest in human ecology. Hoxmark's article, and literature I have received concerning a new journal to be called Human Ecology, make me fearful that the field will be irreparably damaged "at birth." There is an important field that could be called human ecology. I would like to see social scientists and ecologists exchange ideas to their possible mutual benefit. But there are real dangers in either side thinking that they can lightheartedly apply the others' findings.

GEORGE F. CARTER

ISAIAH BOWMAN SCHOOL OF GEOGRAPHY,
JOHNS HOPKINS UNIVERSITY,
BALTIMORE, MARYLAND

¹ Hoxmark, G. 1951. The International Olympic Games and the influence of climate on human energy. Ecology, 32: 151-153.

REVIEWS

TEXTBOOK OF MODERN POLLEN ANALYSIS¹

This book embodies a brief and concise discussion of the methods and principles of pollen analysis and its application to the reconstruction of late Quaternary vegetation. The work and data are pointed largely toward and derived from northwestern Europe, with little mention of American workers. Only 15 of about 160 citations refer to papers on pollen analysis in North America. The book is apparently written for the beginner in pollen analysis and is restricted almost entirely to the basic principles and essential methods of this paleobotanical field. A brief history of pollen analysis in Europe is presented. A chapter on the morphology of pollen grains is well written, emphasizing those characteristics pertinent to pollen identification. Special attention is given to sculpture, including a key to sculptural types, with illustrations. Production and dispersal of pollen grains are considered with relative percentages for a few anemophilous pollen types based upon their capture in pollen traps. The influence of air currents and weather conditions upon pollen dispersal and sedimentation from the atmosphere is pointed out. Two chapters are devoted to peat types and the use of symbols for them. The authors distinguish between peat as chiefly of autochthonous and sediments as largely of allochthonous origins. No attempt is made to classify peat types, except hydrologically. Limnic, telmatic, and terrestrial peats are defined. Sediments are described by the Scandinavian terms of "dy" and "gyttja" formed in dystrophic and eutrophic lakes respectively. A total of 44 symbols is suggested as standard for peat and sediment types.

A chapter on field techniques offers little or nothing in procedures that the average careful worker would not naturally use. Several

methods for preparation of peat for pollen analysis are reviewed with a few original suggestions and ideas. A few types of pollen diagrams are presented, with a brief discussion as to their relative merits and the use of percentages based upon arboreal and nonarboreal pollen. The "fossil forest map" used to depict regional distribution of forest types for a given period of time is shown. Perhaps one of the best chapters is that on the interpretation of pollen diagrams in which over and under representation of species are evaluated. The obvious sources of error are considered and their applications to European problems. A chapter is devoted to the possible application of several statistical methods, with sampling and irregular fluctuations of the curves especially considered. The value and results of these statistics, however, seem hardly commensurate with the amount of work involved. The application of pollen analysis to archeology, climatic cycles, geological events, chronology, paleoecology, human prehistory, and other problems is briefly discussed.

No drawings of specific pollen grains are presented. Morphology of pollen grains is schematically shown, with principal types portrayed diagrammatically. Two types of pollen keys are given, and a sample of the perforated key card for one species. A master key defines 22 pollen classes based upon morphological characteristics, each of which is illustrated. The other is a key to northwestern European pollen types of families or genera, based upon the study of more than 1000 plant species. Both entomophilous and anemophilous species are included. Although this book is not as comprehensive and complete as Erdtman's "Introduction to Pollen Analysis" it clearly discusses and presents the problems and general methods of pollen analysis, and should be of considerable value to the beginning pollen analyst.

HENRY P. HANSEN

OREGON STATE COLLEGE,
CORVALLIS, OREGON

¹ Faegri, Knut, and J. Iversen. 1950. Textbook of modern pollen analysis. 168 pp., 17 figs., 9 plates. Copenhagen: Ejnar Munksgaard. Dan. kr. 16,-.

VERTEBRATES—THEIR LIFE AND HARD TIMES¹

This is a unique and valuable book, with a few eccentric features. It is introduced as (1) "an attempt to define what is meant by the life of vertebrates and by the evolution of that life," and as (2) "an attempt to give a combined ac-

count of the embryology, anatomy, physiology, biochemistry, paleontology and ecology of all vertebrates." On quick second thought the author disclaims any desire to apply himself exhaustively to the second purpose, and it is not a fair criticism of the book to say that it contains no embryology or biochemistry, little physiology or ecology and not enough anatomy or paleontology to serve as a text for both or either.

¹ Young, J. Z. 1950. The life of vertebrates. xv + 767 pp., 496 figs. New York: Oxford University Press. \$8.50.

What he has done is to make a free and effective selection from all these artificially delimited fields and from genetics and natural history, toward an end both less vague and more useful than his first stated purpose. With an extraordinary wealth of illustration, he shows how the genic constitution of the phylum repeats and repeats itself through general anatomic patterns of great stability while undergoing ceaseless and rather frequent minor changes upon which the outer world, itself in flux, can react selectively; so that after varying lengths of time and at unpredictable periods the older forms of vertebrates are replaced by newer ones and perish, and the phylum progresses toward more intricate and more delicately adapted forms.

This is old stuff, of course. But the natural histories pay little attention to the story of evolution, the anatomies neglect natural history, the fossil-catalogs leave out as much anatomy and natural history as possible, the genetics books are concerned chiefly with today's happenings and the evolution books make no attempt to display the whole phylum and its history. This book fits a real need. It is not only an excellent survey of the biology of vertebrates, it is the most readable and thought-provoking general account of vertebrate evolution yet published.

The peculiarities of the volume are understandable when one thinks of the task that any one man undertakes in bringing off such a job at this stage in the development of biology. Since practically all readers are specialists, the problem of selection of materials so as to please even a majority is probably insoluble, even without the Procrustean tyranny of a one-volume limit.

To this reviewer for instance it is surprising to find that the readers of the book are assumed to be completely ignorant of stratigraphy and the geologic time scale but at the same time to have already a solid foundation of classic morphology and genetics. While the bulk of the book is technical and sprinkled with undefined biological terms the first and the last chapter will be instinctively skipped by most readers, as inconsequential or repetitive. General conclusions turn out to be such sobering principles as "Evolutionary change is not always obviously associated with environmental change, though it may be so" (p. 736).

It can also be said that the book lacks symmetry and is full of surprising omissions and conclusions. Taxonomic groups are progressively treated in their own chapters, and there is a very useful table of classification for each group. But Edentate mammals are considered in such detail that their table is longer than that for the entire realm of Actinopterygii. Nearly twice as much space is given to the tetrapods as to the burgeoning fishes of the aquatic $\frac{7}{10}$ of

the globe. Each main group is considered anatomically, but the chapters on cyclostomes and elasmobranchs have much more anatomy stuffed in (with no mercy shown the lay reader) than seems to contribute to the purpose of the book, while more and more extensive attention to subgroups of the higher vertebrates crowds out more and more anatomy from the later chapters, until it all but disappears in the whopping 200 pages allotted to mammals. (The author promises a second volume more adequately covering this last group.)

In physiology, homeostasis is mentioned a number of times as a great and liberating evolutionary achievement, but it is never analyzed into the wonderful and intricate systems of interacting biological systems from which it arises. On the other hand, the various mechanisms for control of chromatophores are examined at length. Visual apparatus is much discussed, even to the detailed revelation of the reactions of an excised eel eye to various drugs, but vertebrate ears are relatively slighted. Brain anatomy is regularly referred to, but considering the amount of light it throws on normal behavior patterns at the present state of knowledge it might as well have been left out. Contrariwise, digestive physiology is all but omitted, though it has clear and diversified relations to the life of animals.

In genetics, there are references to population cycles, to geographic variations and race-circles, and to various aspects of the natural selection processes. On the other hand, the range of variation of structure and physiology within a single wild or cultivated species is an elementary evolutionary gambit that could well have been illustrated in detail in any number of vertebrates, but the subject is never approached directly.

The only point in stretching out such a list is to show the difficulty of selecting for a single volume of such bold inclusiveness. Somehow the author has brought together the points of view of the old Cambridge Natural History, Kükenthal's *Handbuch*, Goodrich's "Structure and Development," Romer's "Vertebrate Paleontology" and other familiar sources, and shaped them to an integrated picture of evolution as we know it. Included also are a whole chapter on the fishing industry (!), solid sections on swimming mechanisms of fishes and the flight of birds, on special adaptations to other forms of locomotion and to feeding, on the breathing of birds and whales, on courtship, breeding and migration in birds (though little of these aspects of fish behavior), adaptive radiations in many groups, and other materials too numerous to mention but clearly pertinent for "defining the life of vertebrates".

In the early chapters on the emergence of vertebrates from unknown precursors, the author builds freely upon a foundation of practically nothing, as is customary even three generations after Haeckel, but he states the alternatives openly and is frank about his logical processes. This refreshing honesty is particularly felt in the later sections of the book dealing with the Cenozoic evolution of the "well-known" groups of horses, elephants, etc., where the predicament is too much material rather than not any. In general the author asks the reader to understand the limits of present knowledge and the existence of alternative hypotheses. This

is an outstanding service and by prevalent textbook standards well beyond the call of duty.

The book is bulky but not heavy, and being printed on non-glossy paper can be comfortably read at night. Most of the illustrations are clear but a few seem to have become murky through over-reduction. There is a well constructed index. The six pages of references are mostly to texts and other secondary sources. The author's style is smooth, direct and genial throughout.

W. W. BALLARD

DARTMOUTH COLLEGE,
HANOVER, N. H.

BEETLES AND FUNGI¹

The biologist and the ecologist interested in the interaction of all forms of life will find an interesting field of study opened up in this volume. The authors made intensive field studies in six months of the summer and autumn of 1946 concerning the inter-relationships of beetles and fleshy, coriaceous and woody fruit-bodies of macro-fungi (Mushrooms, toadstools and conks) in the region of the Vienna Woods in the eastern part of lower Austria near Vienna.

The book is divided into four sections. The problem to be studied is introduced in the first. The fungi studied are considered a union in the vegetation pattern of the region and the relationship between them and the beetles is considered under the general heading of fungus-biocoenose or fungus-zoocoenose.² Collecting and study techniques are described and discussed. A brief description of earlier work on the relationship of beetles to fungi is given. A generalized statement of the fungus aspect of the area for the seasons studied is given with reference to earlier more detailed work on this subject by the junior author and his students, especially Friedrich and Leischner-Siska. Average monthly temperature and its departure from a 160 year average, and total monthly precipitation and its departure from a 50 year average are tabulated. Most of the fleshy fungi studied in the project are considered mycorrhizal and this point is discussed briefly.

Five stages in the development and deterioration of a fleshy fungus fruit body are considered important:

1. Young, fresh: Early stages of development.
2. Growing, fresh: Maturing of fruit bodies, height of development.

3. Oligosaprobe: Mildly rotting as a result of action of snails and insects.

4. Mesosaprobe: Rotten through action of larvae.

5. Holosaprobe: Quite rotten, tissue dead, discolored.

The second section of the book develops the field study techniques in the form of descriptions of results of each field trip. Each field trip is described from the point of view of the field conditions, the fungi found and their condition, and the beetles associated with them listing the numbers of beetles by sex. A description of the "beetle-biocoenose" with notes on factors of substrate conditions, climatic conditions, succession of beetles, etc., is given. For instance, in a dry aspect of the "fungus-biocoenose" species of Staphylinidae are absent but Collembolae are richly present in sporophores of *Russula* species.

The third section of the book gives an annotated systematic account of the Coleoptera collected during the study. The 4,041 specimens in 176 species and forms and 22 families are first listed in tabular form indicating the quantities obtained from the two principal collecting areas.

The fourth section takes up problems of beetle-fungus sociology. As indicated by the predominance of females in certain fungi these fungi are considered "brood fungi," while the same fungus or other fungi act as "station fungi" and serve as "food fungi" for other beetle species.

Considerable space is given to a discussion of the chemistry of the fungus hosts of beetles. 31 types of odors are described and fungus species listed for each. pH values of pressed sap are given for 30 species of fleshy fungi ranging from *Paxillus atrotomentosus* pH 4.32, to *Lycoperdon gemmatum* pH 6.64, mostly taken in the fresh mature condition. Over a period of 10 days pH values of pressed sap from 3 species

¹ Otto Scheerpeltz und Karl Höfler. Käfer und Pilze. 1948. 351 pp., 19 text figures, 9 plates. Wien, Austria: Verlag für Jugend und Volk. 54 shillings (approx. \$2.00).

were obtained daily. Initial readings were between pH 4 and 5, final readings for specimens kept at 37° C fluctuated around pH 10, while those kept at 0° C fluctuated around pH 8. A comparison is presented between insects and fungi and insects and *Arum nigrum*. A detailed account of the taste and smell sensory mechanisms of the concerned beetles is presented.

Concerning the dependence of beetles on fungi three classes are set up:

Mycetobionts—beetles restricted to fungi.

Mycetophilous—beetles which prefer fungi.

Mycetoxenous—beetles which may assume a fungus habitat, but have other habitats as well.

A number of species, genera and generic groups are cited for each of these environmental reactions, the third having the greater number of species studied.

Following Braun-Blanquet (1928) a five pointed fidelity scale is presented:

Fidelity V—Fungus true (pilztreu)—Mycetobionts

IV—Fungus strong (pilzfesten)—Mycetophilous

III—Fungus friendly (Pilzhöhlen)—Mycetoxenous

II—Fungus wanderer (Pilzvagen)—Mycetoxenous

I—Fungus visitor (Pilzfremden)—Mycetoxenous.

For the first two groups the reader is referred to the discussion of the mycetobionts and mycetophiles for a list of characteristic species; for the last three groups the reader is given a list of species with notes on their peculiarities.

For certain species of fungi studied the beetles are listed systematically, the numbers of individuals of each species are tabulated for each collecting trip and this information is totaled for beetle species and collecting trip. For instance, for the non-fleshy, wood inhabiting fungus *Trametes gibbosa*, 235 beetles were collected between July 6 and Dec. 3. These included 29 species in 8 families. The largest number of species (11) was obtained on Oct. 19; the largest number of individuals (49) was obtained on July 6; the beetle species represented

by the largest number of individuals was *Octotemnas glabriculus* Gyllh. with 81 specimens for the period of study. For the fleshy fungi *Collybia platyphylla* was found to have 776 specimens of 21 species in one family group. Studies were started on June 29 and the 15th record was taken on Sept. 14. *Gyrophaga joyioides* was represented by 638 individuals throughout the period. 14 species were taken on June 29 and 177 specimens were found on July 31.

The possibility of a fungus-beetle symbiosis is considered in connection with this group of fungi and arguments in its favor are presented through anatomic, cytologic and histologic studies of beetles. In addition to some original observations the literature is relied on heavily in this connection.

Just as phases of succession of insects have been differentiated on decomposing flesh, dung and excrement, so the authors differentiated five phases of succession in their study of all data accumulated. Single phases and combinations of phases can be named from characteristic beetle genera or generic groups. In many fungus species some of these phases are absent. The following is quoted from the authors:

"In summary we ask: How does the study of the animal associations in fungi fit into general animal sociology?

"The macro-biotype of the forest includes manifold types of life. Within it are distinguished micro-biotypes in which characteristic small animal associations live: tree-trunks, animal dens, birds' nests, animal droppings, plant and animal remains. However, the fungi form the most frequent of these micro-biotypes as special types. They are well delimited, rich in food, chemically and ecologically well characterized as a substratum for life. Still they have hardly been touched systematically. That they are not all colonized similarly, but show a considerable chemical and ecological diversity, as well as furnishing shelter and food for a great variety of types and sociologic variations of biological communities, has been proved by our studies."

WM. BRIDGE COOKE

DEPARTMENT OF PLANT PATHOLOGY,
WASHINGTON STATE COLLEGE,
PULLMAN, WASHINGTON

WILD ANIMALS IN CAPTIVITY¹

Dr. H. Hediger, Director of the Zoological Gardens of Basle, Switzerland, presents in this

¹ Hediger, H. 1950. Wild animals in captivity, an outline of the biology of zoological gardens. Trans. by G. Sircom. ix + 207 pp., 33 figs., 6 tables. London: Butterworth. U. S. distributors: Academic Press, New York. \$6.00.

book an excellent example of how basic theoretical knowledge from the science of ecology can be usefully applied to practical problems. It should be of interest to research workers in the fields of conservation and wild life management and to students of animal behavior and sociobiology as well as to the staffs of zoological gardens and to the interested lay public.

The author follows the method of taking documented information from scientific literature and applying it to the common problems found wherever animals are artificially confined. These problems chiefly involve space, sociality, feeding, breeding and parasites.

He points out that the living space of wild animals is often quite limited because of territoriality or a restricted home range, and that these natural boundaries can often be replaced by artificial barriers with little disturbance to the animals. The problem of reducing the flight distance to conform to a small area can be met by taming, and some further reduction of space can be achieved by reducing the needs of the animal as, for example, in food getting. Space needs can be cut down somewhat by reducing environmental stimulation, but this may result in an environment which is so barren that the animal does not have enough to do and begins to show abnormal behavior in the form of stereotyped movements. Hediger suggests a richer environment with perhaps the inclusion of training and performance.

The subject of sociality is extensively treated and the importance of social organization to the well-being of a group is emphasized. This, the reviewer may point out, is a principle which should be recognized in game management, particularly where an attempt is made to introduce animals into a vacant territory. It is preferable to have a naturally organized group, but if not, organization must be developed in non-harmful ways. Crowding has the effect of producing a rich social environment and consequent hyper-reactivity, which is particularly seen in fighting and sexual behavior. Probably for this reason Hediger tends to somewhat overemphasize the dominance order as compared to other types of social organization such as mother-offspring attraction, leadership, *et cetera*.

He points out that the dominance order can be extended to include more than one species of

animal, and that consequently man is frequently included in the social organization of animals. In such a case it is essential, for obvious reasons, that the particular representative of the human race who is involved should assume the alpha position in the dominance order.

In his section on hyper-sexuality, Hediger includes the phenomenon of breeding out of season as well as sexual behavior, but points out that there is considerable evidence of departure from seasonal breeding even among wild animals. In his section on feeding he brings out the importance of certain experiments in social facilitation and the fact that this does not apply to every species.

From a critical point of view there is but one major suggestion for improvement which could be made. The author makes almost no use of the facts and theories of psychology except for reference to W. Fischel, whose work is little known in this country. American scientists will find the bibliography a rich mine of references to interesting European work, but somewhat poorer in regard to work published in English. The translation by G. Sircom is only fair and there are some laughable mistakes such as translating the German "Stier" or bull as "steer," and many examples of poor word order and punctuation. However, it is for the most part clear and readable, even for a nontechnical reader.

After interesting chapters on the practical problems of zoos, Hediger ends with a statement of the scientific responsibility of the zoological garden which goes far beyond exhibition, a point of view which might well be more widely disseminated than it is among those in this country who have to do with the management of zoological gardens and wild life exhibits.

J. P. SCOTT

ROSCOE B. JACKSON MEMORIAL
LABORATORY,
BAR HARBOR, MAINE

BEES¹

Suitable for both lay and technical readers, this book gives a straightforward account of the gist of nearly four decades of intensive investigation on problems indicated by the title. In substance it is the text of three lectures given by Professor von Frisch at Cornell University, The American Museum of Natural History, and the University of Minnesota, during a lecture tour of the United States in the spring of

1949. Like the lectures, the book is a model of scientific discussion for a mixed audience of scientists and laymen, interestingly presented in a direct, succinct and clear manner. It is an attractive book, cleanly printed and well illustrated.

This is the first inclusive account in English of the author's discoveries on a whole set of complex and difficult problems concerning the honey bee, including both results previously brought together in the author's "Aus dem Leben der Bienen" (now in its fourth edition) and more recent findings. The new book is valuable not only because of its content of ori-

¹ von Frisch, Karl. 1950. Bees—their vision, chemical senses, and language. 119 + xiii pp., 61 figs. Bibliography. Ithaca: Cornell University Press. \$3.00.

ginal scientific results, but also because to an appreciable extent it gives the reader a comprehension of the methods and thinking of an outstanding scientist at work.

An ecological question concerning the relationship of bees to flowering plants stands out in Chapter I, on "The Color Sense of Bees." Von Hess had drawn the erroneous conclusion that bees, since they collected in the green and yellow-green bands in his preference tests, must have a visual system equivalent to that of a color-blind human eye for which these are the brightest areas of the spectrum. Von Frisch showed that bees can distinguish wave-length stimuli visually, although the bee's color sense does not duplicate man's. Bees are red blind, for one thing. As Kühn found in extending this work with spectral lights, bees can differentiate Yellow, Blue-green, Blue, and Ultraviolet qualitatively. This is a significant set of facts for ecology.

Valuable discoveries by von Frisch and others have followed, concerning flower adaptations and distribution; the role of birds, adequately red-sensitive, and of red-sensitive butterflies, in pollinating certain flowers not visited by bees; the finding of an ultraviolet visual sensitivity in bees and many other insects which makes possible their visiting ultraviolet-reflecting blossoms which are red or otherwise colorless to insects; chemoreceptive functions closely related to vision in flower-visiting, and so on. For ecologists, there developed a picture of bees and flowers closely and mutually interrelated in evolution, as selective factors. "One can see that the colors of flowers have been developed as an adaptation to the color sense of their visitors."

Further questions about flower-visiting led to the author's pioneering work on chemoreception, discussed in Chapter II, "The Chemical Senses of Bees." Here, as in other chapters, readers learn how difficult scientific problems can be approached through a simple yet adequate methodology, guided by insight and ingenuity. Not only the sensory physiology of bees, but also questions concerning the evolution of flowering plants, receive clarification in these concise discussions.

The story of comb-dancing by honey bees and its significance for flower-visiting, first reported by von Frisch about 30 years ago, is presented in Chapter III, "The Language of Bees," and in an appendix. But the "dances" cannot be considered alone. The effect of the finder bee upon the hive concerns a whole system of processes involving behavior, scent-gland function, chemoreception and odor-conditioning, and others based on the properties of bees in relation to flowers. Ecologists in particular will note the significant fact that finder bees, returning from flowers often at great distances, regurgitate from the honey stomach nectar containing

flower perfume, unreduced in intensity by flight unlike substances carried on the body surface. The role of the scent-gland secretion is involved both in hive arousal and the finding of specific food places. Because of such relationships, secondary bees normally are not only aroused in the hive but may be specifically influenced in their foraging behavior.

The principle topic of the third chapter is the dancing of returned finder bees on the comb, long an unexplained phenomenon for which von Frisch's work has indicated the significance. The dancing, first of all, has a general arousal function, and also transmits olfactory stimuli from scent-gland secretions and from perfumes carried by finders. But von Frisch has demonstrated other functions beyond these. When steps are taken to rule out olfaction, dancing is still effective in specific ways. From results reported in 1946, von Frisch has corrected his initial interpretation of the "round dance" as a specific stimulus for nectar-gathering bees, the "wagging dance" as specific for pollen gatherers. In his terms, the round dance "announces" food at a nearby source, the wagging dance food at distances greater than 50 or 100 meters. But the wagging dance "tells" more. First of all, other bees are "informed" as to distance, which is "indicated" by a decrease in the number of wagging turns per unit time with increasing distance. "The time or the effort needed to reach the food seems to be the basis for the bee's estimation of distance"—since for example a head wind on the return slows the dances whereas a tail wind quickens them. In some manner, secondary bees are able to "understand the meaning of the dancer's rate of turning and can perceive the distance they must fly to reach the food."

The wagging dance can have another effect, recent experiments show: from it secondary bees "learn the *direction* in which they must fly." The basis is an orientation of the finder bee to directed light, the "light-compass" effect first reported for ants by Santschi and later for bees by Wolf. The surprising result found by von Frisch for bees is that, on the comb in the dark, the direction of the wagging run with respect to the vertical corresponds to the direction of the food place with respect to the sun. For instance, if the straight run is upward on the comb, "this apparently means 'The feeding place is in the same direction as the sun,'" if down, "'Fly away from the sun to reach the food.'"

An interesting problem is revealed by this shift from visual terms to those of gravity on the dark comb, involving intersensory transposition, not unknown in invertebrates although better studied in vertebrates. The straight median run in the dark somehow depends on gravity, for it does not occur when the comb surface is

laid horizontally (in the dark). Von Frisch does not pursue the problem, but remarks simply "We may be sure that this meaningful relationship has developed gradually, like other abilities, in the course of the history of the species."

As for the bees which are aroused by the dancing on the comb, they "recognize the angle of the dance relative to gravity, and in flying out to the food they remember this angle and relate it to the position of the sun." At any rate, the secondary bees somehow are directionalized through the dance, for (with odor controls) their subsequent behavior bears a significant relationship to it. In one of the tests (at 250 meters), of 257 bees: 125 reached the actual food place, 95 diverged no more than 15° to either side, and the rest diverged no more than 45°. Unfortunately, the writer of the book's jacket description overlooked this part, or he could not have misinterpreted the author's results by stating that other bees go to "the exact spot . . . even if it is as far as three miles from the hive."

The dances, and particularly the wagging dance, are a remarkable adaptation which greatly increases the efficiency of bee foraging. How are we to explain them and, in particular, their effect upon secondary bees? In view of von Frisch's precautions to exclude olfactory cues in the critical experiments, the finder bee's behavior during the straight median run must somehow provide the cues. But when one observes the dance situation in the motion-picture record² or on the comb of an observation hive (through red glass), no immediate solution is apparent. Other bees are seen crowding excitedly around the finder during her run, hurrying after or beside her during the double-loop phase or shifting along in various positions during the straight median run, often axially placed and frequently oriented toward her abdomen in this last phase. Von Frisch himself has said in a recent publication, "I do not know by what means the bees can appreciate the direction of the dance." In his major publications on this topic (see *Zoolog. Jahrb., Zool. Physiol.*, 1921, 38: 1-68; also *Experientia*, 1946, 2: 397-404), he has used the word "Sprache" in quotes, and there is no reason to believe that expressions of his such as: the wagging dance "tells" . . . and other bees are "informed" . . . (reviewer's quotes) are intended to suggest an anthropomorphic interpretation of his findings. It seems regrettable that, inevitably, some read-

ers will conclude that such an interpretation is intended by the context.

In this book, as in his scientific papers, von Frisch reports his evidence without any systematic explanation of its psychological meaning. Actually, his results demonstrate a correspondence between the behavior of finder bees and of secondary bees in certain specific situations. The results do not, however, provide a basis for any particular theoretical explanation of the casual nexus between these parallel sets of events.

As Dr. Griffin says in the *Foreword* to this book: "Von Frisch does not present us with vague or mystical speculations but rather with phenomena which, however astonishing they may be, are nonetheless concrete and readily observed." In view of this statement, this reviewer considers it unfortunate that the *Foreword* offers a vague psychological interpretation which goes considerably beyond the evidence in Chapter III of the book. It is not correct, as is implied, that "complex" behavior (as this certainly is) is necessarily "intelligent" in a higher-level sense. The reviewer, in his own studies on insect learning and "instinctive" phenomena, has been impressed with the capacity of insects for exceedingly complex behavior. Cases were studied which had been cited as examples of higher mental capacities in insects. However, investigations directed specifically at psychological analysis showed clearly that the complex behavior was carried out without benefit of higher level (i.e., mammal-like) processes.

It is assuredly not imperative to insist upon holding a *simple* explanation (i.e., one assuming lower-level psychological processes) provided this is demonstrated to be less adequate than a more presumptive one. Although this reviewer accepts the evidence of the book and of the von Frisch experiments, he cannot agree with the implication in the *Foreword* that "higher mental faculties" are involved. Nor can he fall into line with the recurrence of this thought in the statement that "We shall now be obliged to readjust our thinking about animal behavior in the light of these findings and the implications that flow from them." Other kinds of implications also flow from these findings. Let us readjust our thinking appropriately as new evidence warrants a logical rearrangement of our previous concepts about phenomena, but let us not leap to extreme readjustments on a basis of analogies and impressions.

This reviewer obtains from the von Frisch results an indication of a very complex, but nevertheless insect-like, bee-like mode of communication, rather than a human-like, really symbolic set of language processes. The gestural symbols of man are learned and are modifiable through experience, whereas the dances of the bee seem rigid and unstable under uni-

² von Frisch, K. *Dances of the Bee*. 16 mm., 850 ft. This film, with English subtitles and a printed lecture in English, is the original von Frisch motion-picture record, now being distributed in the U. S. by Wilner Films, P.O. Box 231, Cathedral Station, New York 25, N. Y.

versally similar extrinsic conditions. They are a product of a long-term biological evolution, it would appear, rather than of cultural processes. What the finder actually transmits to the secondary bees in the wagging run is still an unsolved problem; however, as a psychologist, this reviewer doubts that, when known, the transmission processes will meet the accepted psychological criteria of "symbolic communication." No previously studied case of insect communication has met these criteria.

The book ends with a fascinating sequel to the previous discoveries. Tests described in Chapter III show that finder bees (observed on a horizontal comb) dance not only with respect to direct sunlight but also to light from a patch of sky. Experiments with filters show that light polarization is involved. In the Appendix

are reported further investigations bearing on this phenomenon, performed since the 1949 lectures. Through the use of an ingeniously devised "artificial eye," von Frisch has demonstrated that the single ommatidium of the bee's eye with its 8 sensillae functions as a differential light-polarization analyzer, permitting orientation with respect to particular brightness patterns of the sky. Thus we stand, the author says in closing, "at the threshold of new problems."

Thanks are due to Dr. Donald Griffin, whose initiative and efficient management made possible both the 1949 lectures and this valuable book.

T. C. SCHNEIRLA

DEPARTMENT OF ANIMAL BEHAVIOR,
AMERICAN MUSEUM OF NATURAL HISTORY,
NEW YORK

ECONOMICS OF NATIONAL AND WORLD FISHERIES¹

This book presents the available knowledge on the environment, the biology and the economics of the North Carolina fisheries. As a summary of these local conditions it will serve a most useful purpose; similar local summaries should be available for all regions of our fisheries. But this book has a significance far beyond its local usefulness.

Dr. Harden Taylor brings to this study very unusual qualifications: a thorough understanding of both theoretical and applied economics, a vast and successful experience of both production and distribution in commercial fisheries, and a wide experience in fisheries biology. From these unique qualifications, we should expect a most valuable contribution and the result exceeds our expectations.

The section on fisheries economics, for which Dr. Taylor is individually responsible, has been extended beyond the bounds of North Carolina. It includes an analysis of the industry in the whole of the United States and draws confirmatory evidence from Europe and Canada.

The characteristics of the fisheries industry, the forces at play, are explained. Food fish find their market as competitive items among the surprisingly constant per capita food consumption. As compared with competing foods, fish is the cheapest to produce; but because of high costs of distribution and difficulties in marketing, it rapidly loses its initial advantage. The economic well-being of the fishermen and of the industry have only the vaguest relation to the size of the catch; in the case of the Great

Lakes fishery, the financial betterment of the fishermen has been associated with a serious decline in the catch. By and large, economic and not biological factors determine whether the industry shall thrive. The possibilities and difficulties of improving the situation have never been more clearly stated.

To the fisheries biologist, the most bitter pill to swallow will be the relationship between fisheries production and the business cycle. Over the period 1921-1940, the total fisheries production of the United States "faithfully followed the turbulent business cycle." During this period the catch and populations of individual fish fluctuated dramatically; yet these great natural changes left no mark on the total fish catch of the country. The total catch was determined by nation-wide economic trends.

For 150 years the cry of "depletion" and "overfishing" has been with us. The fisheries had to be "conserved" and innumerable restrictions were placed upon fishing. Most of these restrictions decreased the efficiency of the fisherman, raised the cost of production and discouraged enterprise and initiative. "*Fisheries management* by public regulation is little more than vain presumption arising from rivalries and jealousies among the fishermen and sportsmen and designed principally to assuage them." Though over the last seventy years the total fish catch has fluctuated with economic conditions, its general trend has been to keep pace with our rapidly increasing population. The total fish catch per capita of population is the same today as it was seventy years ago. What then is meant by "overfishing"? Can it really occur in our oceanic fisheries?

Fisheries management has, from time to time, been rationalized by various theories. At the

¹ Taylor, Harden F. and others. 1951. Survey of marine fisheries of North Carolina. xii + 555 pp. Chapel Hill: University of North Carolina Press. \$10.00.

turn of this century we had the "brood-stock" theory and fish were to be conserved by preserving the breeding individuals. Ample evidence exists, as for instance the phenomena of dominant year classes, that the relationship between the size of the brood stock and that of the future population is complicated and even qualitatively unknown. Yet for generations this theory completely dominated administrative thinking and is still an article of faith. About twenty-five years ago a new theory, that of "optimum catch," came into prominence. This simple concept, that a fishery should be operated so as to produce the best results, is one with which it is difficult to quarrel. Let us consider what happens when these theories are applied to practical fisheries management.

Fishes have been regarded as separate species, each to be observed separately and with no recognition of each as a part of a community with the most complicated inter-relations. Each species is regarded as something static from which man can withdraw just so much; the adjustments which must take place both within a species and between species are not investigated. While we have known for generations that enormous natural fluctuations can and do take place, the operation of fisheries management is predicated upon the assumption that the activities of man are the only variables which

need be considered. Then "catch-per-unit-effort" as a measure of the population, is used to indicate the effect of the fishery. Throughout this volume there are numerous cases of enormous fluctuations in fish populations. In few of these is there any reason to believe that human operations have been the cause; in many, such an interpretation is impossible. Here catch-per-unit-of-effort does not measure the effect of the fishery, but, in an unsatisfactory way, the extent of the natural fluctuation. This book, explicitly and by inference, stresses the importance of natural fluctuations and rejects orthodox "optimum yield" philosophy. Yet, the theory is so deep in our acceptance that we find, on page 135, "The best indication of an overfished population is in a decrease in catch-per-unit-of-effort."

Dr. Taylor's analysis should provoke much needed clear thinking in the muddled theory of fisheries management. How much and how far his views are to be accepted will be the subject of controversy. It is to be hoped that this book will relieve the careful study which it so richly deserves. No more provocative work has appeared in this field in recent years.

ERNEST F. THOMPSON

BINGHAM OCEANOGRAPHIC LABORATORY,
YALE UNIVERSITY,
NEW HAVEN, CONNECTICUT

MICROCLIMATOLOGY ¹

This book is a translation of the second edition of the author's "Das Klima der bodennahen Luftschicht," published in Germany in 1942. The need for such a book covering the field of microclimatology in the English language has long been felt. Dr. John Leighly had translated the first German edition for the U. S. Soil Conservation Service for limited circulation, mostly restricted to official government use.

The book is built around a very comprehensive plan. It covers nearly all the climatic elements and the modifications they undergo because of their contact with the surface of the earth. Starting with the basic factors of radiation, its absorption and transformation by soil, snow, and water surfaces, the author proceeds to trace the climatic influences exerted by heat conduction and eddy diffusion. The variations induced by locale in such meteorological events as frost, dew, fog, and evaporation are thoroughly discussed within the larger setting of the complicated temperature, humidity, and heat

exchange phenomena in the bottom layer of the atmosphere.

The variations caused by topography, human activity, and plant cover are presented in great detail. All of these influences are illustrated by a vast amount of observational material, much of it from the pioneering studies of the author, who has spent a lifetime of research on the subject matter. A whole section is devoted to his particular favorite topic of forest climate.

The role of man as a destroyer of natural microclimates and creator of new ones is covered, as well as the conscious attempts to combat artificially adverse microclimates. In this connection, the chapter on city and housing climate is rather abbreviated. The author is content with a brief summary referring mainly to the monographs of Kratzer, Brezina-Schmidt, and others. There are other deficiencies, especially in the fields of air-pollution microclimate, cave climate, and theoretical analysis of microclimate.

Throughout the book there are a great many references culminating in a bibliography which comprises nearly fifty pages. Unfortunately, the latest reference is to work published in 1947. Hence a great many important U. S. publica-

¹ Geiger, Rudolf. 1950. The climate near the ground. xxi + 482 pp., 179 figs. Cambridge, Mass.: Harvard University Press. \$5.00.

tions such as those by Thornthwaite, Wolfe, and others are not covered.

Some of the shortcomings of the book cannot be laid to the author. In a rapidly advancing science a translation appearing eight years after the original is bound to be out of date. The fact that Dr. Geiger is about to finish the third German edition is sufficient proof for this statement. The revisions that the author made in the English text are too slight to be called a new edition.

The translation in general leaves much to be desired. It is not, as a good translation should be, a re-creation of the original in another language. There is no space to point out the many slips that appear on comparing the German version (of which there is more than one copy in the U. S.!) with the English. They range from annoying trivia (e.g. reference to the "Imperial" Weather Service of the German

Republic, a mistranslation of "Reich"), to misleading phrases, as in Figure 176, where the word *area* appears for *exposure*, or when "Haushalt" is translated as *content* instead of *budget*, or where *dry sod* appears instead of *bare soil*.

On the other hand, the print and make-up of the American edition is superior. An especially commendable job has been done on the re-lettering of the figures.

Even though the translation regrettably omits the German subtitle "A Textbook of Microclimatology" the book is likely to be very useful to students. To the research workers in the field it will be most welcome as a summary of the literature and as a reference compendium up to the middle of 1940 decade.

H. E. LANDSBERG

RESEARCH AND DEVELOPMENT BOARD,
WASHINGTON, D. C.

THE BIOGEOCHEMISTRY OF VERTEBRATE EXCRETION¹

In an unprecedented effort to determine the distribution and concentration of nitrogen, phosphorus, and other elements and compounds laid down as a result of the excretory activities of sea birds and certain mammals, Professor Hutchinson has succeeded memorably.

His work comprises 554 quarto pages, 137 figures, 56 tables, and text of the order of a quarter of a million words. Its bibliography lists nearly a thousand consulted publications, which date from the year 1154 to 1945 or later. Twenty-one of these are anonymous, and the sources depart so widely from the ordinary scope of scientific literature that the author's labor has in part resembled that of historian rather than naturalist. An index fills 34 pages. The table of contents, comprising all headings and main subheadings of the volume, is so descriptively analytical that reference to particular areas, aspects, or problems is greatly facilitated.

The monograph opens with a discussion of the biological and geophysical conditions of guano deposition, and then takes up regionally, and in satisfying detail, the famous nitrogenous deposits of the western coasts of continents, and the phosphatic guanos of Pacific atolls, the Australasian district, the East Indies, the Indian Ocean, the Atlantic and its adjacent seas, including localities as peripheral as the Falkland Islands which, together with New Zealand, are the stations farthest from the tropics to exhibit

phosphatization due to bird colonies. After considering general aspects of avian guano deposition, the author turns to cave guano, mainly though not exclusively a product of bats. He lists and adequately describes the sites on all the continents and a large number of islands. Curiously, there is no mention of Bermuda, which has extensive limestone caverns from which quantities of ancient bird remains have been reported. The final section, except for the important summary of previously unrecognized conclusions, relates to the comparative chemistry of guano minerals.

From the restricted points of view in which the reviewer might offer criticism of Hutchinson's magnificent accomplishment, he finds little to question. One fault, however generous, lies in the undue respect that the author shows for much ornithological taxonomy. This is expressed by his acceptance of trinomials that have little or no significance in nature. In countless instances it would have been preferable to acknowledge a species merely as a species, rather than to lend an unearned finality by employing, for example, such subspecific names as *crissalis*, *fuliginosa*, *oahuensis*, *serrata*, *somalensis*, etc., for as many ill-distinguished populations of the sooty tern (*Sterna fuscata*). There are also certain misidentifications of sea birds. Thus a petrel (*Puffinus griseus*) attributed by Stresemann to the Chilean nitrate fields (p. 112 of Hutchinson) has since been shown to be the young of a gull (*Larus modestus*).

Apart from such matters, the text contains a few understandable redundancies and various misprints of geographic and proper names, of

¹ Hutchinson, G. E. 1950. Survey of contemporary knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion. Bull. Amer. Mus. Nat. Hist., 96. xviii + 554 pp., 16 pls. \$10.00.

which the frequent repetition of "Arica" with a final accent is the most flagrant. There is also an occasional reference to an authority omitted from the bibliography, e.g. "Clarke, 1924."

The diverse nature of the evidence—climatological, oceanographic, archaeological, biological, chemical, and mineralogical—and the inductions drawn, endow this work with the fascination that pertains to all good sleuthing. As applied to the foremost among areas of nitrogenous guano, Hutchinson meticulously disposes of the hypothesis that the Peruvian deposits are of vast age. On the contrary, they are a result of a young climatic régime that dates from only the first or second millennium B.C. This is not to deny the possibility of older cycles that have left few traces. A footnote (p. 71), refers to a bed of ancient guano on Central Chincha Island, perhaps marking an unconformity and lying beneath three meters of aeolian sand. Since the publication of Hutchinson's paper, Arnold and Libby (Science, 113 (2927): 111-120, 1951) have determined the age of a sample of this from the C^{14} content, and have concluded that it is older than 19,000 years.

Hutchinson states, upon stratigraphic grounds, that the well-recognized climatic cycle of slightly less than seven years, along the Peruvian coast, is both young and "non-persistent," even in human terms. There is no evidence of it, he holds, prior to 1864. Despite his careful consideration, the reviewer questions whether the last word has been said on this subject. The *año de abundancia* (referring to a cyclic lushness of desert vegetation) seems to have long been a familiar term in northern Peru (Murphy, R. C. 1941. Hispanic American Historical Review, 21 (1): 3-28). Furthermore, the late Professor Edward H. Berry (in Murphy, R. C. 1926. Geogr. Rev. 16: 26-54) held that periodic "wet years" have left their mark in the stratigraphy of northwestern Peru since Tertiary time.

The stages of guano production appear to be related to a secular zonation of climatic controls moving from south to north along the west coast of South America. These may be correlated with what has happened in west Africa, and possibly with similar climatic successions in the western Pacific. Hutchinson, at any rate, is the first to offer adequate comparison of conditions in these widely separated areas. There seems to be a relation between the cycles of South America and South Africa to the extent that the depressions in Africa anticipate those of the Peruvian coast by a year or more. The South African guano deposits also agree with those of South America in being of rela-

tively recent age.² It has been possible to treat the Peruvian climatic cycle in detail from about the year 1618 to date. During most of the period for which data exist, the curve of guano production is in full agreement with other information relating to fluctuations in the guano bird population.

The Chilean deposits are mainly post-Pleistocene, and chemical evidence shows that they are certainly older than those of the Peruvian islands. This is interpreted as meaning that the Chilean coast was climatically suitable for guano production before the Peruvian coast became arid enough to permit storage of nitrogenous guano. Even within the past two centuries, a decline has continued in the importance of guano-producing centers of northern Chile and southern Peru as compared with those of central and northern Peru. (Incidentally, the theory of the ultimate origin of Chilean nitrate from guano involves at least one insuperable difficulty, namely, that of accounting for the disappearance of the phosphate.)

Circumstances parallel to those observed in Chile and Peru are postulated for some of the central and western Pacific islands. It is very unlikely that large deposits could ever have formed on islands receiving annually more than 1000 mm. of rainfall. There are indications in the existing deposits that the rain belt has undergone a shift from south to north within the past few thousand years. This is put forth by Hutchinson as a working hypothesis to account for chemical conditions as he finds them.

The important guano deposits were quarried away during the 19th century before any adequate account of them had been written. During this period about half of them were still growing, whereas the others were due to ancient but post-Pleistocene bird colonies. The Pleistocene deposits are, however, strikingly more massive than those of post-Pleistocene time. Circumstances were evidently then more favorable for guano deposition than are known anywhere today outside the Pacific coast of South America. It is likely that oceanic productivity was greatest during declining glaciation, when nutrients stored throughout a long prior period were being released to the upper layers of the water. The interglacial periods may therefore have been times of enhanced oceanic richness. Hundreds of thousands of years under general conditions of the present day would be required for building the guano on Nauru Island. Under

² A recent report, particularly important because it cites 25 earlier publications not included in Hutchinson's bibliography, is the following: Liesegang, C. 1950. Die Guanowinnung auf den Inseln und an der Küste Südwestafrikas. Erdkunde, 4, parts 1-2: 35-43.

existing Peruvian conditions, however, the immense Nauru deposits could accumulate in a very few thousand years. The areas of the richest guano beds today are arid for the same reasons that the adjacent seas are highly fertile.

Phosphatic guanos arise from decomposition, the solution of both the original and the secondary constituents, and the subsequent migration of the solutes. Such changes are the result of moist conditions, and phosphatic guanos are, of course, far more abundant than nitrogenous guanos, which endure for long periods only in a very dry environment. From chemical, stratigraphic, and meteorological evidence, Hutchinson concludes that two periods of intense phosphatization may have been as characteristic of the Pleistocene as was glaciation.

The maximum total amount of phosphorus removed from the ocean and deposited as phosphatic guano on tropical and subtropical islands does not exceed 10,000 metric tons per year. If we add nitrogenous guano to this, the total estimate would be 18,800 tons. Since a vastly greater quantity of phosphorus enters the sea annually from the land surfaces, it follows that the removal of phosphorus by birds is of no significance in the general geochemical cycle of the element.

Fluorine is a common element in the deposits of the elevated, phosphatic, coral islands, but the problem of its origin remains unsolved. No theory as to its source is without objections. Good determinations of fluorine throughout well described profiles on a series of islands are needed as the next step toward conclusions of great interest.

In discussing the life history of contemporary guano birds, which represent a "climax" in as true a sense as a forester might use the word, Hutchinson's text attains its peak of ecological brilliance. On the Peruvian coast the total population of the three or four principal species may normally be about ten million. Within the Republic, 147 islands and 21 mainland localities now produce guano. The important birds are all members of the order Pelecaniformes which, at least in that part of the world, ordinarily retain their excrement until it can be deposited on the nesting ground. This is known

not only from observation, but also from statistical evidence. The food intake agrees closely with the weight of excreta at the nest. It is this characteristic, of course, that makes the Peruvian cormorants, boobies, and pelicans the guano birds as contrasted with many other marine fowl of the region. One advantage of their curious specialization is that the water of their extensive feeding grounds does not become opaque when the vast flocks are fishing. There is no evidence that guano birds drink any appreciable amount of sea water. Enough potassium, chloride, and sodium is present in their solid food to supply more than the observed amount in the guano.

Hutchinson calculates that an annual guano crop of 150,000 tons requires the ingestion of at least 1,460,000 tons of fish by the birds during the same period. He suggests, however, that the birds convert no more fish into guano than is consistent with an indefinite persistence of all the parts of the eco-system concerned. No such margin of safety relates to the fish-meal exploitation, which should never be allowed to take the place of the fortunate natural industry in Peru. There are abundant indications that large insular bird colonies, far from reducing a commercial take of fish by competition, may actually increase the catch by a process of biogeochemical concentration, in other words by increasing the fertility of the waters close to their nesting grounds.

In times of great avian mortality, such as coincide with the "seven-year" weather cycle in Peru, it is not necessary to assume that the normal food of the guano birds is dead or absent. It may merely be confined beneath the thermocline that then develops. At such times the anchovies may approach the surface only at night when the birds are not able to feed upon them.

Despite the wealth of Professor Hutchinson's scientific findings, here only faintly reflected, his monumental synthesis poses quite as many questions as it answers. It will long provide a rich lode of problems for doctoral theses—and in half a dozen different disciplines!

ROBERT CUSHMAN MURPHY

AMERICAN MUSEUM OF NATURAL HISTORY,
NEW YORK

THE LOVES OF THE CARD INDEX CARDS¹

This book is addressed "to all serious students of human behavior; be they professional special-

¹ Ford, Clellan S., and Frank A. Beach. 1951. Patterns of sexual behavior. Foreword by Robert Latou Dickinson. viii + 307 pp., 16 figs. Harper & Brothers and Paul B. Hoeber, Inc. [no place of publication]. \$4.50.

ists or otherwise." Its aim is to place in perspective the sexual behavior of man and that of animals, and also to provide a comparative anthropological background for the type of North American activity so curiously documented by Dr. Kinsey. Sexual behavior is defined for the purpose of the study as "behavior involving stimulation and excitation of the sexual organs."

The book considers the nature of coitus in man and animals, the kinds of stimulation involved, the circumstances of sexual activity, sexual attractiveness, the various kinds of sexual partnership known in man and animals, homosexuality, extraspecific mating, autoerotic activity, the ontogeny of sexual behavior, the female sexual cycles, the role of hormones in sexual behavior and other aspects of the physiology of sex. The word "love" occurs in the index only in connection with magic; perhaps this is as it should be.

The non-human material is primarily mammalian; the human is derived partly from the surveys made in recent years in North America, but chiefly from the predominantly preliterate peoples studied by anthropologists with sufficient care to permit the information to be incorporated into the Human Relations Area Files (formerly Yale Cross Cultural Survey). Such material as might have been available from the ancient world is rejected, not because it would be unreliable, but for the odd reason that the sources are too likely to be aristocratic. Consideration of the vast mass of Japanese, Indian, and one might add Persian, Arabic and European erotica, is omitted, according to the almost incomprehensible foreword by Dr. Dickinson, for lack of space.

The comparative mammalian material is extremely interesting and the authors deserve great credit for presenting a new and fairly consistent account of the main physiological and behavioral peculiarities of the sexual life of *Homo sapiens* as a species. These peculiarities, some of which are foreshadowed in the lower primates, involve a liberation from hormonal control, so that sexual activity can occur at any time during adult life, and the tendency for the mates to approach each other, and for mating to occur, face to face, which tendency, though by no means universal, is prevalent enough to have had a profound effect in sexual selection, emphasizing the breasts and face and also leading to far more effective clitoral stimulation than is likely to occur in any other mammal. It is reasonable to suppose that these changes from the normal mammalian pattern of coitus, still exhibited by the great apes, are connected both with the erect posture of man and more remotely with the development of binocular vision. True sexual climax or orgasm is unknown in infra-human female mammals and its occurrence in women in at least some, though probably not all cultures, provides a further specifically if not universally human characteristic. It seems indeed just possible, though the authors are much too careful to suggest it, that some physiological evolution is actually going on here, a matter of peculiar interest not only practically, but also because, in every other respect, no important physical evolutionary change

seems to have occurred in any man for some time. It is rather disappointing that Ford and Beach give us no thoughts on the significance of the hymen, a curious and specifically human structure.

The comparative material is, as has been indicated, practically limited to mammals. The seasonal development of sexual activity in its full biological setting is hardly considered; the ecologist will find little or nothing about territorial phenomena. The very important problem of how mating is normally maintained intra-specific is quite inadequately discussed. The lack of any detailed discussion of the sexual behavior of birds is particularly striking in this connection. It is also disappointing to find so little material that might bear on sexual selection as an evolutionary agent in man. Ford and Beach point out that far more attention is paid to beauty in women than in men, presumably a relatively unusual situation in the animal kingdom. They indicate what a very great diversity of taste exists in regard to feminine beauty, but give inadequate attention to the selective significance of this. The whole subject of sexual selection requires vastly greater study than it has been given; recent workers have far too often taken the attitude that because certain sexually dimorphic patterns are involved in aggressive territorial display, sexual selection is an exploded theory. It is, however, very difficult to see how, for instance, the characteristically human ear lobe has evolved except through sexual selection as a structure in which ear-rings can be inserted. A careful study would probably reveal a number of similar cases providing *prima facie* evidence; a few of these cases then might be amenable to further more rigorous exploration. Meanwhile, one could have wished that the material indicating how, in some cultures tall women and in some short, in some cultures fat women and in some thin, are preferred, had been accompanied by somatological data indicating how the average morphology may vary with the preference. The possible selective significance of the curious maxima in sexual desire in women, before and after menstruation, when no conception is likely to occur, also poses problems of particular interest to the demographer.

The parts of the book dealing with comparative human material are far less satisfactory than are the discussions on a more purely physiological level. The initial definition of sexual behavior and the methods of research and presentation lead to an atomistic point of view from which nothing appears in its full functional sequence. The whole book appears to be buoyed up by a hope that some significant correlations will be born of the matings of the file cards, but so far these unions seem to have been disappointingly infertile. There is a curious con-

clusion that biting, scratching and similiar violent forms of love-making are habitual only in cultures, here termed permissive, that allow a good deal of adolescent sexual freedom, though the inverse proposition that such freedom implies the development of violent forms of sexual play is not true. Whatever the significance of this correlation may be among the preliterate cultures studied by Ford and Beach, "Phoebus amorous pinches black," belong to a culture that would probably not have been regarded as permissive in the Human Relations Area Files. The only other statistical conclusion that appears, seems to be that the occurrence of sexual interest in the breasts, which is not universal in human cultures, is not correlated with whether the breasts are habitually covered or left bare. The atomistic inadequacy of the approach is strikingly apparent when the covering or uncovering of the breasts is considered. As that learned Jesuit, Father Alberti, pointed out long ago in his unpublished tract on this question, everything depends on the prevailing circumstances. A Bavenda woman takes off her shapeless cotton blouse and appears in the full dignity of a sepia torso and a carefully beaded skirt because she is home in her village and has left the white man's town where certain regulations are enforced. The Virgin, in some mediaeval representations of the Last Judgment, opens her robe and cries in agony for all mankind *Pili, aspice ubera quae te lactaverunt*. An Italian peasant woman bares her breast in a railroad coach full of men for the excellent reason that her baby is hungry. A chorus girl at the Casino de Paris does the same to lend erotic charm to a theatrical spectacle. Exposure to public view of the same special part of the body, covered a short time before, is involved in all these instances, yet functionally the acts are extraordinarily different. It is extremely curious to see that a generation of functionalist

anthropologists, who criticized Sir James Frazer for wrenching divine kings out of context, though when he wrote around the Mediterranean he really knew what he was writing about, should give place to a statistical generation whose members are now taking tiny bits of sexuality out of context without the slightest shame simply because they have an IBM machine rather than a classical education to help them.

The authors of *Patterns of Sexual Behavior* claim to have "consistently eschewed any discussion of rightness or wrongness of a particular type of sexual behavior." Actually, it is probably impossible to free any statements about the matters they consider from all normative overtones. It is extremely unlikely that most of the material in the book would be taken, by any large group of readers, with the same emotional calm as would result from a discussion of the evolution of suture pattern in Jurassic ammonites or a statement about the decrease in ionic radius with increasing atomic number in the rare earth elements.

It is impossible to avoid implying value judgments, and the only value judgment that is validly implied is one that is based on a consideration of at least a carefully weighted sample of all the evidence. It may, in fact, be doubted whether it is really of value to present comparative material based mainly on the statistical and exclusively non-functional study of preliterate societies to a reading public who are believed to need the dimensions of the human genitalia in inches and fractions thereof (which to this reviewer is definitely pornographic) rather than in millimeters. Readers accustomed to the metric system will, however, find ways of using the book profitably.

G. E. HUTCHINSON

YALE UNIVERSITY,
NEW HAVEN, CONNECTICUT

COPEPODOLOGY FOR THE ORNITHOLOGIST

Recently in the course of preparation of chapters on the zooplankton for a forthcoming comprehensive work on all aspects of limnology, it has been necessary to study in detail a considerable number of papers on the freshwater copepoda, particularly the Calanoida and planktonic Cyclopoida. During the course of this study it became apparent that the literature contained a number of disconnected facts of considerable evolutionary significance. Some of these facts provide striking analogues to phenomena recorded in other groups, particularly the vertebrata. Since it is probable that the somewhat more detailed account prepared for my book will not come to the attention of ornitholo-

gists and other students of terrestrial ecology, and since early publication is desirable to stimulate further research on these matters, the preparation of the following summary seems justified.

Selective and non-selective feeding. The calanoid copepods feed largely by filtration. In this process the antenna is used as a screw to produce a water current, from which food particles are filtered, largely by the maxillae. The details of the process have been elucidated in detail by Storch and Pfisterer (1925) and more recently by Lowndes (1935). It has commonly been supposed that the process of feeding must, under these circumstances, be entirely auto-

matic. Quite apart from some evidence of diversified feeding habits to be derived from a study of the structure of the mouth parts, Lowndes demonstrated directly selective feeding by supposedly non-selective species. Large particles can be rejected by the simple expedient of separating the maxillae, so letting the particle pass the filter. Certain substances added to the water can be avoided and field evidence indicated that even *Eudiaptomus gracilis* (Sars), a species commonly regarded as quite unselective, could seek out benthic desmids when living in a pond soupy with *Kirchneriella*, which was entirely rejected. Burckhardt (1935) found that the males of *Eurytemora affinis* (Poppe) rejected a greater proportion of *Coscinodiscus* in favour of smaller diatoms than did the females though there is no significant difference in size between the sexes. There is some morphological evidence that the maxilla is less well adapted as a filter in some *Diaptomidae* than in others and Lowndes found that even in the obvious filter feeder *Eurytemora velox*, there is often evidence in the faeces of predation on other Crustacea. We may expect therefore that, since what is large for a small species may be small for a large species, the food of two species of different sizes will not be identical and that, at least in some cases, the most confirmed filter feeders will exhibit some selectivity in the kind of neighbourhood they select for their filtering operations.

Size differences in associations of closely allied species. It has been observed (Hutchinson, Pickford and Schuurman 1932; Hutchinson 1937) that in the playa lakes or pans of semi-arid regions, the plankton often consists of a single species of *Daphnia* and two Diaptomid copepods of widely different sizes. In the Transvaal, *Lovenula falcifera* (Lóven) of length 3.5–5.0 mm in temporary less alkaline, and *L. excellens* Kiefer of length 3.0–3.5 mm, usually in perennial and more alkaline, localities are associated with *Metadiaptomus transvaalensis* Methuen of length about 1.9 mm. In Big Washoe Lake, a playa in Nevada very similar to the Transvaal pans, the large *Hesperodiaptomus franciscanus* (Lillj.) and small *Leptodiaptomus tenuicaudatus* (Forbes) similarly co-occur. More complex associations are found in some of the temporary waters of the south-eastern Palaearctic. In the pluvial zone of North Africa, Gauthier (1928) found the immense *Hemidiaptomus ingens* (Gurney), about 5.2 mm long, associated with *D. cyaneus* Gurney about 3.2 mm long and with both *Eudiaptomus numidicus* (Gurney) and *Myxodiaptomus lilljeborgi* (Guerne and Richard) about 1.5 mm long. Similarly in Turkey, where two other species of *Hemidiaptomus* of great size occur, Mann (1940) found *H. brehmi* Mann of length 4.2–5.0 mm associated with *Arctodiaptomus belgrati*

Mann of 0.98–1.24 mm, and *H. kummerlöwe* Mann of length 3.5–4.45 mm with *A. baccillifer* (Köbel) of length 0.87–1.19 mm. It is probable that in Central Asia also the large species of *Hemidiaptomus* always have small associates (Sars 1903). Though the existence of marked size differences is often very conspicuous in temporary waters it is by no means confined to them. Carl (1940) concluded that in the lakes of British Columbia when two Calanoids co-occurred, they are generally separated by a size difference. The most frequent case that he encountered was the association of *Epischura nevadensis* Lillj. of length 1.8–2.1 mm and *Leptodiaptomus tyrelli* (Poppe) of length 1.2–1.3 mm. Gurney (1931) gives two particularly interesting cases of very closely allied species living together being separated by small size differences.

The first is that of the copepods regarded below as two separate species, living together in Loch Ness in Scotland:

	♂	♀
<i>Eudiaptomus gracilis</i>	1.26–1.35 mm	1.4 mm
<i>E. pusillus</i> (Brady)	0.98–1.17	0.99–1.2

The second case is that of the very closely allied *Arctodiaptomus wierzejskii* (Richard) and *A. laticeps* (Sars) which differ only in the most minute characters of certain segments of the antennule. Considering these as a whole, the rather wide range of size variation overlap completely. On the rare occasions when they co-occur they are separable by small size differences. Gurney gives the following mean values for the populations in Loch Moracha, North Uist:

	♂	♀
<i>A. wierzejskii</i>	1.4 mm	1.53 mm
<i>A. laticeps</i>	1.3 mm	1.43 mm

Cases are certainly known in which calanoids of the same size inhabit the same water. Sufficient data however exist to suggest that a diversity of size, probably implying, in view of what has been said about feeding habits, some difference in food, frequently makes possible the co-occurrence of two or more species of Calanoids.

The evidence in the Cyclopoida is less striking because the Cyclopidae include a great many benthic forms. It is therefore possible to have a number of allied species in a lake without their habitats overlapping appreciably. When two very closely allied species occur in the plankton, they tend to be of different sizes. Thus in Lake Toba, Sumatra, Kiefer (1933) records a population of large specimens of the very widespread *Mesocyclops leuckarti* (Claus), the females being about 1.12 mm long, in company with the endemic *M. tobæ* Kiefer of which the females were only 0.7 to 0.8 mm long.

Similarly in Lake Lanao, Mindanao, Philippine Islands, the widespread *Thermocyclops hyalinus* (Rehberg) is accompanied by a smaller endemic species *T. wolterecki* Kiefer (1938).

A comparable case among supposedly benthic species is given by Harding (1942) who obtained four species of *Eucyclops* from Lake Young in Northern Rhodesia. Two of these were new and possibly endemic species, probably derived from *E. serrulatus* (Fischer). They resembled each other and differed from their nearest allies in the much shorter antennae. The most conspicuous difference between the two species of the pair is in size, *E. parvicornis* (Harding) having adult females 1.02–1.06 mm long, *E. spathanum* 0.64–0.71 mm long. The latter species has flattened spines on the pleopods which presumably may also indicate some functional difference.

On account of the less automatic feeding mechanisms of the Cyclopoids, some selection of food seems likely but, though many zoologists have reared Cyclopidae in the laboratory, little is really known of their food habits. What little information does exist in no way conflicts with the idea that larger individuals would not eat exactly the same kind of food as smaller.

The role of size differences in permitting the coexistence of closely allied species of birds and mammals has been stressed by Huxley (1942, p. 280–281) and by Lack (1944). Brooks (1950a) has employed the same idea in his interpretation of the distribution of *Odontogammarus* in Lake Baikal. It is obviously possible that in invertebrates with little metamorphosis and prolonged life histories, competition of adults of the smaller species with sub-adults of the larger species may produce complications. In spite of this and perhaps some other difficulties, the existence of size differences seems to provide one way by which sympatric species of restricted groups of planktonic animals can exist under conditions in which, in general, competition might be supposed inevitably to eliminate one form.

The variation in clutch size in the freshwater Calanoida. When, as in most freshwater Calanoida, the female carries the eggs in an egg-sac, it is easy to observe the variation in the size of the clutch within a given species. Such variation was noted by Schacht (1897) in *Diaptomus siciloides* Lillj. described from Lake Tulare in California as carrying but four eggs, but in the Illinois River having egg-sacs containing up to eighteen eggs. Schacht supposed that since the type locality is a mountain lake, the larger number of eggs carried in the Illinois River is due to higher temperature and better food supply. In some cases, the variation can be quite extraordinary; Mann (1940) records a minimum of 2 and a maximum of 64 in specimens of *Arctodiaptomus bacillifer* from Turkey.

Mean values for whole samples varied from 6 to 60, but the data are inadequate to demonstrate any seasonal trend.

Wesenberg-Lund (1904) found that *Eudiaptomus gracilis*, in most of the Danish lakes in which the species occurred, carried from 25 to 30 eggs in the spring, but only from 6 to 8 during the summer and autumn. Though there was some irregularity in the second half of the year with a possible hint of a second or autumnal maximum, the main and very striking feature of the variation is the rise to and fall from the well-marked spring maximum. Rzóška (1925) found a similar variation in Poland, where *E. gracilis* carries 22 to 28 eggs in the spring and but 4 to 6 in July. Within a given region, there is, however, also some variation from lake to lake, for Wesenberg-Lund found that although the variation in the clutch-size in the population in Furesö¹ followed the same seasonal pattern as in the other lakes, the absolute number of eggs per clutch is smaller, falling from 14 to 20 at the time of the spring maximum to 4 to 5 at the time of the minimum. Von Klein (1938) in an admirable study of the Crustacea of the Schleensee found that *E. gracilis* carried a mean clutch of 11.0 to 11.4 in April. This sank to a minimum of 3.0 on August 2 and rose to an autumnal maximum of 8.8 on November 5. Later, but five or six eggs were carried through the winter. It is evident that the variation follows the variation in abundance and reproductive capacity of *Daphnia cucullata* in the same lake. Though it is tempting to regard variations of this sort as controlled by food, von Klein points out that *Diaphanosoma* and *Ceriodaphnia*, which are filter feeders like *Daphnia*, rise to a maximum between the *Daphnia* peaks and the periods of maximum egg production by *E. gracilis*. Gurney, also writing of *E. gracilis* considers that in Britain, fewer eggs are carried by females in large lakes than in ponds; these remarks are in part due to a confusion about *E. pusillus* Brady but are no doubt partly correct. Again it is tempting to suppose a greater food supply in the smaller shallower waters.

In *Eudiaptomus graciloides* Wesenberg-Lund noted a variation comparable to that exhibited by *E. gracilis*, save that in the case of the former species so little reproduction occurred after the late spring that individuals carrying any eggs in the summer were very rare. In Esromsö, at the beginning of the breeding season in April, at a temperature of 3° C. the females carried

¹ The Furesö population is, by an obvious misprint, referred to *E. graciloides* in that part of the English summary that refers to clutch size; reference to the Danish text or to the earlier paragraphs of the English summary make clear that *E. gracilis* is meant.

from 7 to 9 eggs, in the first week in May at 8° C., 10 to 12 eggs, at the end of May at 13° C., 4 to 5 eggs. The very small number of females reproducing later in the year generally carried 4, 5 or 6 eggs. In other less well studied lakes, the same sort of variation occurred; occasionally up to 16 eggs may be carried in spring.

A similar variation in egg number during the reproductive season is exhibited under entirely different circumstances by *Phyllodiaptomus annae* (Apstein) in the lake at Colombo, Ceylon (Apstein 1907). Here, when reproduction begins in June the females carry about 30 eggs, but this number sinks progressively as the population rises to a maximum and falls again, till in September when little reproduction is occurring and the species is becoming scarce, the egg-sacs contain only seven to nine eggs.

Cases such as that of *Eudiaptomus graciloides* in which the clutch size increases and decreases while a marked rise in temperature is occurring and cases such as that of *Phyllodiaptomus annae* where marked changes occur at a time when little variation in temperature is to be expected, suggest that a variation in food-supply is more likely to underlie the phenomenon than is a change in the physical environment. It is to be noted that such variations in clutch size are not limited to the Calanoida but occur in the Cyclopoida and in certain pelagic Cladocera also. Wesenberg-Lund noted a decline in the number of eggs carried by a species of *Cyclops* that he refers to *C. strenuus* from 40 to 50 in the spring to 20 to 30 in the summer. He also noted a large decrease in the number of the brood carried by *Daphnia* as the season progressed. Later work by Brooks (1946) strongly suggests that in the lakes of Connecticut, the summer individuals with small broods are indeed somewhat starved. Slobodkin (verbal communication) finds that food-supply controls fecundity in *Daphnia obtusa* Kurz.

Wesenberg-Lund claims that in the three copepods that he studied, not only does the clutch size decrease, but the egg diameter increases as spring gives place to summer. He gives measurements only in the case of *Eudiaptomus graciloides* where the spring eggs have a diameter of about 120 μ and the summer eggs of from 160 to 200 μ . Assuming a spherical form, the volume of the spring eggs must be about $9 \times 10^5 \mu^3$ and of the summer eggs $21-42 \times 10^6 \mu^3$. Thus a summer clutch of 4 will contain as great a volume of eggs as will a spring clutch of from 9 to 18. These considerations at least suggest that the variation in clutch size throughout the breeding season is not necessarily merely a direct effect of starvation, and, at least in species in which reproduction occurs on a large scale throughout spring and summer, part of the variation may prove to

have some adaptive meaning. Wesenberg-Lund suspects that the large summer eggs may hatch at a naupliar stage later than the first. Several workers have noticed that the limited number of nauplii produced in spring survive better than do the summer nauplii which are responsible for the small rise in population in late August and September. It is therefore not unlikely that early in the season when the population is expanding into a lake rich in food, individuals producing many small eggs will leave most descendants, while later in the year when the population is larger and the food supply less, it is desirable to increase as far as possible the individual life expectancy of the nauplii produced. This case appears to be comparable to some studied by Lack (1947, 1950) in birds and provide a loose temporal analogy to the geographical variation in egg number and size noted by Svårdson (1949) and Määr (1949) in *Salmo alpinus* (cf. Brooks 1950b).

Specific differentiation in clutch size. Brehm and Zederbauer (1902) recorded up to seven eggs in the egg-sacs of *Eudiaptomus gracilis* in the lakes of the Austrian Alps in summer, but usually only four in winter. They later (1906) observed that the winter population differed from that present in summer in having the spinous process at the tip of the twenty-third segment of the geniculate antennule of the male much reduced. Haempel (1918) noted a comparable or greater reduction in Austrian populations referred to *gracilis*, but elsewhere this supposed cyclomorphosis has not been observed (Brehm 1927). Gurney (1931) specifically states that he has looked for such temporal variation without success in the perennial populations of *E. gracilis* in the Norfolk Broads. However, in Loch Ness, Gurney describes a small slender form which he refers to *gracilis*, though noting that Brady has described just such a form as *pusillus*. It is distinguished from typical *gracilis* which has also been found in Loch Ness not only in its slenderer build and slightly smaller absolute dimensions but also in carrying from one to four eggs, the usual clutch consisting of two. It also differs in the male in having the apical process of the twenty-third segment of the geniculate antennule reduced, just as in Brehm and Zederbauer's supposed winter form of *gracilis*. It is most reasonable to suppose that two species² are involved, dif-

² There is a possibility that dimorphism within a single species is really involved. Several South American diaptomids are supposed by Wright (1938) to be dimorphic; a comparable case in the genus *Neodiaptomus* is treated by Kiefer (1939) by giving both forms specific status. Most cases of supposed dimorphism are doubtless due to the adult moulting (Gurney

fering in minute morphological characters, in the average number of eggs per clutch in any given locality and, at least in the Austrian Alps, in the breeding season. It appears probable from Gurney's figures that the eggs of *E. pusillus* are slightly larger than those of *E. gracilis*, though this requires further investigation. The co-occurrence of two hardly distinguishable species differing in reproductive physiology is reminiscent of similar phenomena in the genus *Coregonus*, for instance, in the lakes of Sweden where sympatric species, differing mainly in breeding season have been described by Svärds-son (1949).

Fugitive species. In ecological succession of any sort, a series of species becomes established early in the process; almost any member of this series is destined to become extinct locally by the time the climax is reached. This is, in general, due to the fact that the earlier species have certain properties, often related to dispersal and ecesis, which the later species lack, while the later species are always able to displace the earlier in any competitive process. In an undisturbed landscape in which successional stages are present over a relatively small area, the species limited to the earlier stages of succession are obviously extremely local.

It is conceivable that species, not obviously associated with successional stages on a large scale, may actually be able to exist primarily by having good dispersal mechanisms, even though they inevitably succumb to competition with any other species capable of entering the same niche. Such species will be termed *fugitive* species. They are forever on the move, always becoming extinct in one locality as they succumb to competition and always surviving by reestablishing themselves in some other locality as a new niche opens. The temporary opening of a niche need not involve a full formal successional process. Very small, seemingly random changes in the physical environment might produce locally a new niche suitable for the fugitive, or some unfavorable circumstance might cause the temporary disappearance of a competitor from such a suitable niche over a small region. Any such change would give the fugitive species its chance, for a time, until some more slowly moving competitor caught up with it. Later it would inevitably become extinct, but some of its descendants could occupy transitorily a temporarily available niche in some other locality. A species of this sort will enjoy freedom from competition so long as small statistical fluctuations in the environment give it a refuge into which it can run from competitors. Although it is usual in large scale ecological succession for the species of one stage to differ considerably

from those of another, there is nothing in the concept of fugitive species to suggest that this will be so. It is in fact likely that many fugitive species will be extremely closely allied to their principal competitor, since the two occupy identical niches. One of a pair of sibling species could well be fugitive.

While it is possible that the deductive situation described above is a limiting case, comparable to the bread-and-butterfly of *Alice Through the Looking Glass*, the probable existence of fugitive species is indicated by the appearance of otherwise rare species in artificially constructed habitats such as dams. A case of this sort described by Kiefer (1933, 1938) gave rise to the speculations just set out.

In Indonesia two widespread, and several endemic, species of the copepod genus *Thermocyclops* have been recorded, together with certain species of the very closely allied genus *Mesocyclops*. One of the widespread species, *T. hyalinus*, is distributed through the Oriental region northwestward into the western Palaearctic. The other widespread species *T. decipiens* Kiefer is found throughout the Oriental Region and tropical Africa. The two species are so closely allied that Gurney (1933) placed *decipiens* in the synonymy of *hyalinus*, but Kiefer's (1938) later paper dispels any doubt as to their distinctness.

There is no clear interpretation of the ecological differentiation between *Mesocyclops leuckarti* and the two widespread species of *Thermocyclops*, which permits, for example, *M. leuckarti* to co-occur with either *T. decipiens* or *T. hyalinus* in the plankton of ten out of the eleven lakes in which *M. leuckarti* was found by the German Limnological Expedition to the Sunda Islands. Whatever the cause, it is quite evident that *M. leuckarti* does not compete with the two species of *Thermocyclops* in Indonesia. It would seem equally clear that these two species do compete with each other, for out of thirty-five localities (Heberer and Kiefer 1932; Kiefer 1933, 1938) for *hyalinus* and eighteen for *decipiens* only one is common to the two species. Under most circumstances it is evident that *hyalinus* and *decipiens* exclude each other or have ecological requirements that do not overlap. None of the published data suggest any difference in the range of immediate environmental variables tolerated by the two species. Kiefer, however, points out that while the localities for *hyalinus* appear to be natural, those for *decipiens* include several dams and comparable artificial bodies of water. This indicates that *decipiens* though less common than *hyalinus* must have good powers of dispersal. The whole picture of the distribution would be explained if *decipiens* were a fugitive species in the sense defined above.

1931), but this is not a likely explanation in the present case.

This idea has indeed been applied to the freshwater Copepoda before, by Elton (1927, 1929) who concluded that *Eurytemora velox* Lillj. and *Eudiaptomus gracilis* (Sars) behaved in the way postulated above, *E. velox* being the fugitive species which ultimately and inevitably succumbs to competition with *E. gracilis* when the latter gains an entry to the habitat in which *E. velox* is living. Lowndes (1929, 1930) has disputed Elton's conclusions, and Gurney (1931) notes that the two species can co-occur though he admits the rather frequent association of *E. velox* with artificial waters.

Although statistical presentation makes the very large number of rare species normally encountered in a flora or fauna seem reasonable, it is intuitively not obvious, in view of the fact that some organisms are extraordinarily eurytopic, why most species have to be content with such a limited degree of success. The problem as to why rarity is so common a phenomenon needs more detailed merological analysis than it has been accorded; a too great emphasis on the overall hological or statistical picture may obscure important issues. The above considerations on *fugitive species* are put forward, not on account of their originality, which is inconsiderable, but rather to emphasize in as formal a way as possible, one rather neglected mechanism by which rare species can maintain themselves.

Concluding remarks. By far the most important contributions to ecology and evolutionary theory recently based on the study of the Copepoda are the beautiful series of researches carried out by the Italian school of limnologists on the existence of slight racial differences when both planktonic (Baldi, Buzzati-Traverso, Cavalli and Pirocchi 1945; Tonolli 1949; Baldi, Cavalli, Pirocchi and Tonolli 1949) and benthic (Pirocchi 1947) copepods from different parts of the same lake are studied. Since an admirable review of the matter has recently been published by Baldi (1950) and since the conclusions arrived at are already becoming well-known, it has seemed best in the present note to concentrate on those aspects of copepological research for which some vertebrate analogies exist and which have been inadequately emphasized before.

REFERENCES

- Apstein, E. 1907. Das Plankton im Colombo-See auf Ceylon. Zool. Jahrb., 25 (Syst.): 201-244.
- Baldi, E. 1950. Phénomènes de microévolution dans les populations planktiques d'eau douce. Viertel. Naturf. Ges., Zurich, 95: 89-114.
- Baldi, E., A. Buzzati-Traverso, L. L. Cavalli, and L. Pirocchi. 1945. Frammentamento di una popolazione specifica (*Mixodiaptomus laciniatus* Lill.) in un grande lago in sottopopolazioni geneticamente differenziate. Mem. Ist. It. Idrobiol., 2: 167-216.
- Baldi, E., L. L. Cavalli, L. Pirocchi, and V. Tonolli. 1949. L'isolamento delle popolazioni di *Mixodiaptomus laciniatus* Lill. del Lago Maggiore e i suoi nuovi problemi. Mem. Ist. It. Idrobiol., 5: 295-305.
- Brehm, V. 1937. 3. Ordnung der Crustacea Entomostraca: Copepoda. In: W. Kükenthal und T. Krumbach, "Handbuch der Zoologie," Bd. 3, Hälfte 1, pp. 435-496.
- Brehm, V., and E. Zederbauer. 1902. Untersuchungen über das Plankton des Erlaufsees. Verh. d. zool.-botan. Ges., Wien, 52: 388-402.
- . 1906. Beiträge zur Planktonuntersuchung alpiner Seen. Vehr. zool.-bot. Ges., Wien, 56: 19-32.
- Brooks, J. L. 1946. Cyclomorphosis in Daphnia. I. An analysis of *D. retrocurva* and *D. galeata*. Ecol. Monogr., 16: 409-447.
- . 1950a. Speciation in ancient lakes. Quart. Rev. Biol., 25: 30-60.
- . 1950b. Recent advances in limnology. Ecology, 31: 659-660.
- Burckhardt, A. 1935. Die Ernährungsgrundlagen der Copepodenschwärme der Niederelbe. Int. Rev. ges. Hydrobiol. Hydrogr., 32: 432-500.
- Carl, G. C. 1940. The distribution of some Cladocera and free-living Copepoda in British Columbia. Ecol. Monogr., 10: 55-110.
- Elton, C. 1927. Animal ecology. London: Sidgwick and Jackson. xxi + 207 pp., 8 pls., text illustrated.
- . 1929. The ecological relationships of certain freshwater Copepods. J. Ecol., London, 17: 383-391.
- Gauthier, H. 1928. Recherches sur la faune des eaux continentales de l'Algérie et de la Tunisie. Alger: Imp. Minerva. 419 pp., 3 pls., 6 maps.
- Gurney, R. 1931. British freshwater Copepoda, vol. 1 (Calanoida). London: Ray Society. lii + 238 pp.
- . 1933. British freshwater Copepoda, vol. 3 (Cyclopoida). London: Ray Society. xxix + 384 pp.
- Haempel, O. 1918. Zur Kenntnis einiger Alpenseen, mit besonderer Berücksichtigung ihrer biologischen und Fischerei-Verhältnisse. I. Der Hallstädter See. Int. Rev. ges. Hydrobiol. Hydrogr., 8: 225-306. 2 Tb., 4 fig.
- Harding, J. P. 1942. Cladocera and Copepoda collected from East African lakes by Miss C. K. Ricardo and Miss R. J. Owen. Ann. Mag. N. Hist. (11 ser.), 9: 174-191.
- Heberer, G., and F. Kiefer. 1932. Zur Kenntnis der Copepodenfauna der Sunda-Inseln. Arch. naturgesch., N. F., 1: 225-274.

- Hutchinson, G. E.** 1937. A contribution to the limnology of arid regions primarily founded on observations made in the Lahontan Basin. Trans. Conn. Acad. Arts Sci., 33: 47-132.
- Hutchinson, G. E., G. E. Pickford, and J. F. M. Schuurman.** 1932. A contribution to the hydrobiology of pans and other inland waters of South-Africa. Arch. Hydrobiol., 24: 1-136.
- Huxley, J. S.** 1942. Evolution. The modern synthesis. New York and London: Harper and Bros. 645 pp.
- Kiefer, F.** 1933. Die freilebenden Copepoden der Binnengewässer von Insulinde. Arch. Hydrobiol., Suppl., 12: 519-621.
- . 1938. Die von Wallacea-Expedition gesammelten Arten der Gattung *Thermocyclops* Kiefer. Int. Rev. ges. Hydrobiol. Hydrogr., 38: 54-74.
- . 1939. Scientific results of the Yale North India Expedition: Biological Report No. 19. Freilebende Ruderfusskrebse (Crustacea Copepoda) aus Nordwest und Südindien (Pandschab, Kaschmir, Ladak, Nilgirisgebirge). Mem. Ind. Mus., 13: 83-203.
- Klein, H. von.** 1938. Limnologische Untersuchungen über das Crustaceanplankton des Schleinesees und zweier Kleingewässer. Int. Rev. ges. Hydrobiol. Hydrogr., 37: 176-233.
- Lack, D.** 1944. Ecological aspects of speciation in passerine birds. Ibis, 86: 260-286.
- . 1947. The significance of clutch-size. Ibis, 89: 302-352.
- . 1950. Family size in titmice of the genus *Parus*. Evolution, 4: 279-290.
- Lowndes, A. G.** 1929. The occurrence of *Eurytemora lacinulata* and *Diaptomus gracilis*. J. Ecol., 17: 380-382.
- . 1930. Some freshwater Calanoids. Direct observation v. indirect deduction. J. Ecol., 18: 151-155.
- . 1935. The swimming and feeding of certain calanoid Copepods. Proc. Zool. Soc. London 1935 (3): 687-715.
- Määr, A.** 1949. Fertility of char (*Salmo alpinus* L.) in the Faxälven water system, Sweden. Rep. Inst. Freshwater Res., Drottningholm, No. 29: 57-70.
- Mann, A. K.** 1940. Überpelagische Copepoden türkischer Seen. Int. Rev. ges. Hydrobiol. Hydrogr., 40: 1-87.
- Pirocchi, L.** 1947. Isolamento ecologico e differenziazione di popolazioni di *Megacyclops viridis* Jur. nel Lago Maggiore. Mem. Ist. It. Idrobiol., 3/4: 307-322.
- Rzóska, J.** 1925. Contribution à l'étude des Copepodes de la Grande Pologne. Bull. Acad. Amis des Sci. de Poznan, Ser. B, No. 1: 34-43, 1 pl.
- Sars, G. O.** 1903. On the Crustacean fauna of Central Asia. Part 3. Copepoda and Ostracoda. Annu. Mus. Zool., St. Petersb., 8: 195-232. 8 pls. Appendix. Local faunae of Central Asia, pp. 253-264.
- Schacht, F. W.** 1897. The North American species of *Diaptomus*. Bull. Illinois State Lab., Natural History, 5: 97-203.
- Storch, O., and O. Pfisterer.** 1925. Der Fangapparat von *Diaptomus*. Z. vergl. Physiol., 3: 330-376.
- Svärdson, G.** 1949. Natural selection and egg number in fish. Rep. Inst. Freshwater Res., Drottningholm, No. 29: 115-122.
- Tonolli, V.** 1949. Distribuzione in quota e tempo di entità fenotipiche biometricamente differenziabili, entro la popolazione di *Mixodiaptomus lacinatus* Lill. del Lago Maggiore. Mem. Ist. It. Idrobiol., 5: 317-325.
- Wesenberg-Lund, C.** 1904. Plankton investigations of the Danish lakes, Special part, Copenhagen, 223 pp., 8 maps, 10 pls., 9 tbs.
- Wright, S.** 1938. A review of the *Diaptomus bergi* group with descriptions of two new species. Trans. Amer. Micro. Soc., 57: 297-315.

G. E. HUTCHINSON

 OSBORN ZOOLOGICAL LABORATORY,
 YALE UNIVERSITY,
 NEW HAVEN, CONNECTICUT

BOOK NOTICES

Slotkin, J. S. 1950. *Social anthropology: The science of human society and culture.* xviii + 604 pp. New York: The Macmillan Company. \$4.75. This ambitious textbook attempts to lay down in a systematic manner what is currently held to be "the fundamental theory concerning the nature and effects of human society and culture." Despite its dazzling display of erudition, it is only partially successful. As an orderly anthology of most of the concepts employed in contemporary anthropology and sociology it is not without merit (although probably no one would agree with all of the definitions and statements it contains); and the arrangement of materials concerning the human organism, social groups, and culture reflects more of an implicit "fundamental theory" than is developed in the text. But the manner of presentation—terse and didactic statement of concepts and propositions illustrated by cases allegedly relevant to the subject at hand from the whole range of human society and history—reminds one more of a nineteenth century *omnium gatherum* than of a twentieth century textbook in social anthropology. Major emphasis is devoted to social structures in their static relationships; the dynamic aspects of society and culture receive little consideration. Treatment of the interaction between man and environment is scattered and sketchy, the author being more concerned with man's philosophical attitudes toward the environment than in his concrete relationships with it. Social ecology is disposed of in two pages in the middle of the chapter on social relations. *S. W. Reed.*

Taft, Donald R. 1950. *Criminology: A cultural interpretation.* (Revised edition.) 1950. xiv + 704 pp. New York: The Macmillan Company. \$5.50. Shorter by one chapter than the 40-chapter edition of 1942, this revision retains all of the virtues and faults of the original publication. Among its virtues may be listed an encyclopaedic comprehensiveness in treating of individual, social, and cultural factors surrounding behavior called criminal; a multiple-factor approach to the problem of causation; and a sober realization that criminology is still one of the most chaotic sub-fields of current social science. Its faults are those which characterize the great majority of social science textbooks produced in this country: inordinate length and excessive wordiness, poor writing, and provincial concentration upon American phenomena only. As a reference work it contains a mine of facts and quasi-facts which contribute to the explanation of crime and help to describe penological practices. Readers of this journal may be especially interested in Chap. 10, "The Ecology of Crime: Region and Neighborhood," Chap. 15, "Crime as a Product of the General Culture," and Chap. 18, "A Tentative 'Theory of Crime.'"

Despite the author's efforts to make this "A Cultural Interpretation," the reviewer feels that the original subtitle—"An Attempt at a Synthetic Interpretation with a Cultural Emphasis"—still remains a fairer description of what is actually accomplished in the revision. *S. W. Reed.*

Thompson, Harold. 1948. *Pelagic tunicates of Australia.* 196 pp., 75 plates. Melbourne: Commonwealth Council for Scientific and Industrial Research. This handbook should be of value to any student of the pelagic tunicates and of marine zooplankton in general. The material on which it was based consisted of plankton hauls collected at 304 stations from May 1938 to January 1941 over the southeastern Australian area from the Tropic of Capricorn to the South Australian coast. Although the book was designed primarily as a guide to the identification and occurrence of species in the southwest Pacific it will also be useful to students elsewhere, since many of the species have a wide circumtropical and subtropical distribution. The treatment is primarily taxonomic although the distribution and ecology of the various species are considered. The 75 plates include figures of every species, both reproductions of previously published diagrams and new figures drawn from the Australian material.

The last chapter treats the biology of the pelagic tunicates in general. The salp, *Thalia democratica*, was the form collected in greatest quantity, while *Oikopleura longicauda* was numerically second. *Doliolum denticulatum* was the most abundant doliolid. The north-south distribution of 44 species of Copepata and Thaliacea in the Australian area is diagrammed and the possible use of various species as indicators of changing hydrological conditions is considered. The center of abundance of the Copepata is towards the north although about one-half of the species may reach Tasmanian waters. The unusual appearance of the rarer species in the south would therefore indicate a change in hydrographic conditions. This is true in general of the Thaliacea also, although a few species are more typically southern; the unusual occurrence of these latter forms in the north would be evidence of the presence of colder waters. The pelagic tunicate fauna of the Australian region differs from that of California, Newfoundland, the North Sea and Japan in that species such as *Oikopleura labradoriensis* which occur in moderately cold water are completely absent. Only circumtropical and subtropical species occur. Even in Tasmanian waters no typically Antarctic species have been found. The same characteristically warm water species are predominant in the Australian region as in the East Indies, the Philippine Islands, and southern Japan. *G. B. Deevy.*

ANNOUNCEMENT

BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

In response to the need for a regional journal for the growing volume of marine research along the coasts of the Gulf states, the Atlantic coast of Florida and the West Indies, the Bulletin of Marine Science of the Gulf and Caribbean will be published beginning in March, 1951.

The Editorial Board is representative of the various marine sciences and also of the geographical area:

ROBERT H. WILLIAMS, *Editor*
University of Miami

JOHN H. DAVIS, JR.
University of Florida

LUIS HOWELL RIVERO
University of Havana

DALE F. LEIPPER
Agricultural & Mechanical
College of Texas

NORMAN MILLOTT
University College of the West Indies

HILARY B. MOORE
University of Miami

CHARLES M. POMERAT
University of Texas

LUIS R. RIVAS
University of Miami

WALDO L. SCHMITT
United States National Museum

F. G. WALTON SMITH
University of Miami

Papers dealing with marine biology, physical and chemical oceanography and submarine geology, either directly or indirectly related to the region, will be considered for publication. It is anticipated that contributions will have considerably more than local significance, however, and that the investigations reported will be of general interest to all concerned with the marine sciences.

Papers appearing in the first number include (abbreviated titles): Distribution of oceanic birds, by H. B. Moore; Metamorphosis of barnacles, by H. D. Doochin; Oyster taxonomy, by G. Gunter; Marine borer attack and illumination, by L. B. Isham, F. G. W. Smith and V. Springer; Pelagic cephalopods, by G. Voss; Diseases of oysters, by J. G. Mackin.

Inquiries regarding subscription rates and materials submitted for publication should be addressed to

ROBERT H. WILLIAMS, EDITOR
Marine Laboratory, University of Miami
Coral Gables 46, Florida

